

PALESTINE JOURNAL OF BOTANY

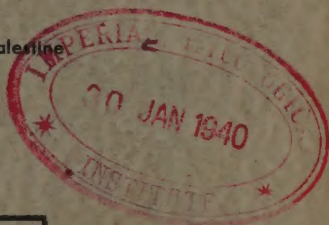
Rehovot Series

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EDITED BY

H. R. OPPENHEIMER and I. REICHERT

of the Agricultural Research Station, Rehovot, Palestine



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Dedicated to the memory of OTTO WARBURG

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PALESTINE
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Rehovot Series

September, 1939

IN MEMORIAM ALEXANDER EIG

By H. R. OPPENHEIMER.

Of the men who will go down to history as the fathers of botanical research in Palestine we have now even lost the third: after AARONSOHN and WARBURG we are mourning the death of ALEXANDER EIG.

This is the heaviest blow we could have been dealt. WARBURG, the considerate, calm, and heavy man of the cool North was our Moses: He has conceived the idea of a science of botany native in Palestine and serving the development of the country. He has lead us to Mount Nebo; he was, however, destined to share but little in the work itself.

AARONSOHN, the fiery child of this country, was our Josua. He laid the first foundations to geo-botany and agricultural botany in Palestine. But, brilliant in so many different ways, he could not fail to scatter his gigantic forces. His early death unfortunately prevented this extraordinary man and scientist from publishing in his life time the bulk of the rich botanical material he had collected.

EIG devoted his extraordinary will-power and exceptional intellectual gifts almost exclusively to botany and erected the building of our geo-botany with surprising speed. An inner unrest urged him to hasten with his work as he may have felt how short a space of time fate was to allot him for it. And now, while he is with us no longer, we find the building complete in its essentials; the plant sociological studies which he has left us unpublished appear to furnish even the roof. Although unfinished and still requiring years of work before accomplished in every detail his work rises proud and impressive be-

fore our eyes. Important, too, are his achievements in organising the Department of Botany at the Hebrew University (after WARBURG's retirement) and as university teacher, and his profound influence on all friends and teachers of botany in this country.

ERG was born the son of a teacher in Minsk (Russia) in 1895. Being of limited means it meant a heavy sacrifice to his father to give his son the training in science and agriculture in which he took an early interest; he therefore sent him to Palestine, when 14 years of age, to study at the Agricultural School of Mikveh Israel. Here, and later at the Herzl School in Tel Aviv, ERG was given his entire education. What knowledge he acquired was sufficient to allow him later to advance into a scientific career on the strength of his own learning. His studies met with much understanding among Palestinian labourers. They enabled him to secure a scanty living as librarian, and later by scientific lectures in the Jewish Labourers' settlements. ERG spent all his spare time in studying the flora of Palestine to which he decided at the age of about 26 to devote his life.

The most varied national currents and movements have been of deciding influence in ERG's intellect, character and education. His youth was marked by the struggle of the Russian middle-class "intelligentsia" craving for knowledge against a Tsarism hostile to popular enlightenment. ERG was in close touch with Russian science until his death; he read Russian literature more than any other and wrote in the Bulletin of Applied Botany, Genetics and Plant Breeding (Leningrad). When he came to Mikveh Israel all the teaching was still done in French language, indeed, this institute under the patronage of the Alliance Israélite Universelle to-day still breathes the spirit of French culture and taste. Here ERG acquired an intimate knowledge of the French language. Later on he became a member of the Société Botanique de France and maintained close relations in particular to the universities of Geneva and Montpellier. Upon entering the Hebrew grammar school Herzlia in Tel Aviv a great and lasting love of the Hebrew language and Jewish culture was aroused in him. Thus he could grow up to be a spiritual member of the Jewish Labourer's Movement which combines national enthusiasm with the socialist sense of personal simplicity, both of them distinct features of ERG's personality. His work under the director-

ship of O. WARBURG (1925—1933) paved his way to a thorough acquaintance with German plant geographical and systematic literature, and brought him into contact with the Botanical Museum at Dahlem and the Herbarium HAUSSKNECHT in Weimar. Many of his papers have therefore been published in German language. Finally, his work in Jerusalem provided him with ample opportunity to approach English Science and to come into contact with the great centre of research in Kew. This influence also made him publish some papers in the *Journal of Botany of the Linnaean Society*. All these connections and bonds together with his travels into various countries of the orient gradually made him a scientist of truly international character.

Ascetic even in his appearance, EIG was one of those, who, regardless of their own welfare, sacrifice their health and wealth to the idea that possesses them. In his appearance he had some similarity with Mahatma GANDHI, and he would hardly have been noticed as a stranger within the walls of a Tibet Monastery. Men of his character and disposition will accomplish great things in life, if given scope for the outward development of their forces. It may even be true that big achievements, especially in the fields of art, science and religion, are impossible without some of the boundless enthusiasm of which these men are capable.

EIG was highly gifted as a scientist and a devoted teacher. He easily assimilated and developed critically Russian, Swiss, French, and American schools of research. Travelling, collecting, studying, and teaching untiringly he was a pioneer of science in the best sense.

When we first met 13 years ago he worked in two rooms of the Agricultural Experiment Station, then still in Tel Aviv. The racks of the herbarium which he had founded together with his friend the early deceased botanist Eliezer FACTOROVSKY were built of raw timber, the library was poor, instruments were lacking, and a single assistant, M. ZOHARY, helped him on his excursions and with the herbarium work. EIG was at that time but a student of the local flora. His first publication on the flora of Palestine (1924) had aroused some interest but he was yet unknown to the botanical world at large. A further paper on the flora of Palestine (1926) still had us little suspect his exceptional talent.

In this bulletin called "A Contribution to the Knowledge of the Flora of Palestine" (1926) he first of all added to DINSMORE's "Jerusalem Catalogue of Palestine Plants" a great number of species and varieties the existence of which had escaped the notice of previous collectors. He further drew the attention of his fellow-men to the great danger which the progressive drying of swamps and development of agriculture constituted to the native flora. He demanded the protection and preservation of nature in which lovers of the country of all races and creeds should cooperate. Now, after his death, this his challenge should spur us all the more into action. Far too little has hitherto been accomplished!

His "Second Contribution to the Flora of Palestine" (1927) shows EIG rapidly developing into a first rank taxonomist. From among the flora of Palestine, which may be looked upon as well explored, he founds several new genera and proves himself a particularly competent judge of involved systematic problems in the families of *Leguminosae* and *Graminaceae* in which he continues until his death to take a great interest. A new genus, *Factorovskya*, is separated from *Trigonella*; many new forms of *Medicago* are described, and the first contributions are made towards a clarification of the systematic position of *Aegilops*.

Immediately after, EIG published his outstanding and fundamental sketch "On the Vegetation of Palestine", with which he gained his spurs as plant geographer. As WARBURG points out in his preface the scanty literature available on the plant geography of Palestine was out of date: for 40 years no publications on this subject had been forthcoming. Basing on his thorough personal knowledge EIG investigates the climatic, edaphic and ethnological conditions of our vegetation, and reviews its types and their relations to neighbouring countries. After that he treats the plant formations in the climatic zones of the Mediterranean and of the oriental Steppe. In conclusion he describes the vegetation of saline and ground-water soils and of cultivated areas (irrigated or un-irrigated).

While EIG was engaged on this work we met again in the Kabbara swamp near Zikhron Yaaqov. Roving through this region, which has since been dried almost completely, EIG and his assistants M. ZOHARY and N. FEINBRUN collected plants doomed to perish in

these localities, such as *Apocynum venetum* L., *Cladium Mariscus* etc. Nearby EIG then discovered *Factorovskya Aschersoniana* (URB.) EIG and studied the interesting vegetation of the mountain slopes. He found there a garrigue, with *Ceratonia Siliqua* and *Pistacia lentiscus* as dominants, which he later recognised as resembling ancient forests found near the Mediterranean coast. Here and there bushes of *Quercus calliprinos*, with *Clematis cirrhosa* climbing to its full height, *Arbutus Andrachne*, *Styrax officinalis*, and wild olives appear as minor elements, while dense undershrub vegetation of fragrant *Salvia triloba* covers what free space there remains between them. Perennials of rare beauty such as *Cyclamen latifolium*, fire red and bluish *Anemone coronaria*, white *Crocus hyemalis* and *Bellevalia flexuosa* complete the picture of this vegetation in spring. Here EIG followed the steps of AARONSOHN whose life-work—as he told me later—he felt himself called to continue.

Meanwhile N. VAVILOV, the great Russian plant geographer and geneticist had come to Palestine in autumn 1927. His visit was of deciding influence on the development of Palestinian botany in general, and of the study of the genetics and taxonomy of the agricultural crop plants and their wild relatives in particular. VAVILOV induced EIG to use his rich experience with the genus *Aegilops* for a monographic treatise of this extremely complicated genus. EIG took up this work with great zeal. He investigated the variability of the species of *Aegilops*, which he studied in cultivation as well, and travelled to Germany and Russia while at the same time WARBURG consulted on his behalf the herbarium of LINNÉ in England. As soon as 1929 EIG published the results of his studies in a paper which comprises 228 pages and secures him a place of honour in the agrostological literature of the world. The deceased in this work proves himself a master of clear distinction between confusingly multi-form types of plants evolved in homologous sequences. Masterly is the way he discovers certain distinctive characters which had escaped other observers: the venation and hairiness of the glumes, the fusion of caryopses and lemmæ, the degree of development of the awns and their progressive reduction, and the mode of disarticulation of the ears at maturity. All this he uses to draw up a natural systematic arrangement of the genus the involved forms of which had defied masters of taxonomy like SIBTHORP and SMITH, JAUBERT and SPACH, and even

BOISSIER. At the same time EIG shows an unusual knowledge of geography, geology and climatology. This enables him in a genetic-plant geographic section to sketch the evolution of the genus from the Tertiary Age onwards and the migration of its forms of which the centre of origin lies in Asia minor, Syria and the islands of the Eastern Mediterranean. EIG's subdivision of the genus into sections has essentially been confirmed by the cytological investigations of SCHIEMANN which were carried out simultaneously.

This book, which naturally could not be appreciated outside scientific circles made his author well-known as a plant taxonomist. EIG who had meanwhile (1929) changed from the Agricultural Experiment Station then at Tel Aviv to the Hebrew University in Jerusalem made an equivalent achievement in the sphere of plant geography with his book "*Les éléments et les groupes phytogéographiques auxiliaires dans la flore palestinienne*". This earned him the degree of Doctor of the University of Montpellier renowned for the sequence of outstanding botanical researches on the plant geography of the Mediterranean countries, which has been carried out there.

In this work, EIG gives a complete plant-geographical analysis of the species constituting the phanerogamous flora of Palestine which he divides mainly into the Mediterranean, the Saharo-Sindian and a third element from the Steppe of Central and South Western Asia called by him the "Irano-Turanian" element.

We shall not discuss this work here at any length as it is simultaneously being reviewed in detail by REICHERT. It may suffice to stress that here EIG has made a masterly contribution to the clarification of long-debated problems. As to the question whether the Sahara should be included in the holarctic or the palaeotropic flora, he decides himself for the former. He tentatively establishes the border lines between the regions with Mediterranean and those with steppic and desert elements in the Syro-Palestinian zone of vegetation.

While this work by EIG was being printed in Berlin we had an opportunity to hear at the Botanical Museum how highly EIG was appreciated in Dahlem. He was no less highly thought of in Geneva, Leningrad, Stockholm, and particularly in Montpellier where he came into close scientific contact with BRAUN-BLANQUET. This extraordinary man's influence became determining for EIG's further develop-

ment as a scientist. He now set himself the task of initiating plant sociological research in Palestine. A detailed knowledge of the plant associations occurring in nature—obscured in Palestine beyond all recognition by human activities—was rightly taken by him to be the key to a clearer definition of boundaries between the distinct phytogeographic districts. By this means he would especially be able to settle problems like that of the boundary between the Sahara-Sindian and the Steppic region in the arid Southern district of Cisjordan (Negueb), the central regions of the Jordan valley, and the western mountain slopes of Transjordan.

On his return from Montpellier in 1931 Eig was full of these ideas. We were then colleagues at the Hebrew University and enjoyed both the most inspiring atmosphere of the Mount Scopus with the view on the Old City of Jerusalem, the Judaeen desert and the Dead Sea. I remember Eig one day stopping in front of the window of my laboratory and enquiring after the work being carried out there viz. a study on the water economy of the mediterranean tree and shrub vegetation. I then believed that Eig's interests continued to centre on systematic botany and that a critical review of the flora of Palestine was what he aimed at in the first place. But in the course of the conversation his ultimate aim turned now out to be the analysis of the ecological requirements of the plant societies found in this country. As a matter of fact Eig was at that time facing the decision in which direction he was to continue his work. Both tasks were so big that one man's life could not suffice to fulfill them. In addition we were at this very moment charged with a third task: to organise university courses with but scanty instructional material at our disposal and in a language which could not yet satisfy the requirements of botanical teaching.

Eig tried to master these three tasks all at once. Although this exceeded the limits set to him by his delicate constitution his accomplishments are truly admirable. Travelling to Syria, Anatolia, and Kurdistan (1931—33) he acquired the necessary knowledge of the plant societies occurring in the countries bordering on Palestine, where they had generally been much less obscured by human interference. Later (1935) he travelled through the Sinai-District as far as Akaba. These journeys markedly facilitated the work of mapping Palestine from a plant geographical point of view by the hypothetical recon-

struction of the natural vegetation which was concluded with the second "Phytogeographical Map of Palestine" published shortly before his death. On these travels he felt his plant sociological work hampered by the lack of systematic monographs on complicated genera. To write these EIG used the vacation and—alas—the nights, too. As the result of his studies we now possess on the one hand comprehensive plant sociological material (including a monograph on the vegetation of the light soils of the Palestinian coastal plain) the majority of which is going to be published only now after his death by his assistant, Dr. ZOHARY in the Jerusalem Series of this journal, on the other hand we have exhaustive monographic studies on the oriental forms of the genera *Astragalus*, *Crepis*, *Anthemis* etc. which have just appeared.

EIG with a Faustian urge for increased and deepened insight thus advanced in both the directions outlined above, and might rightly have said of himself:

"Ever advancing, pride and happiness I seek,
Restless with thirst for knowledge as I am".

ALEXANDER EIG AS A PLANT GEOGRAPHER

BY ISRAEL REICHERT

Dr. ALEXANDER EIG's studies in systematic botany, such as his monographs on *Aegilops* and on the oriental species of *Astragalus*, suffice to ensure him a place of honour in botanical science. But his great original contribution to this science which will—even in generations to come—make botanists refer constantly to his work, undoubtedly lie in the sphere of plant geography. This work is full of interest not only for students of plant geography in Mediterranean and Near East countries but also for whoever engages on problems of general plant geography. The definitions EIG gave of the terms element and region are extremely valuable for the advance of floristic plant geography, even though they did not solve all intricacies of these problems. In the following we shall attempt to outline EIG's original contributions to geobotanical science and to appreciate them.

INFLUENCES

EIG was essentially autodidact. The period of his university studies was no more than a year. His monograph on *Aegilops* and many other papers were written before he had even commenced his studies. We first met EIG when he was only an enthusiastic private collector of plants (1923—1925); we also had the privilege of introducing him to Prof. OTTO WARBURG, who was at the time one of the directors of the Agricultural Experiment Station, of recommending him to the latter for a position at this institute, and later to work together with him from 1925—1929. We therefore had ample opportunity to study closely EIG's development and the various influences which directed his work.

EIG of course received the first impulse to study the geography of plants from nature and the land itself. During the years

preceding his work at the Experiment Station he continuously travelled about the country and systematically collected plants. The wide divergence between the flora of different climatic zones of Palestine which is noticed even by casual observers, attracted the attention of this young and keen-eyed lover of plants. But he only had the opportunity to study these problems intensively when he entered the Experiment Station in 1925. Professor WARBURG appointed him assistant in his Division of Applied Botany and at first supervised and directed his work. Although WARBURG never spent more than 4—5 months of each year in this country, he yet succeeded in arousing EIG's interest for phytogeographical observations required for the agricultural purposes of the Division. But first-rate practical facilities for an intensive study of these problems was only given to EIG when WARBURG in 1926 transferred his comprehensive botanical library from Berlin to the Agricultural Experiment Station. Now EIG was first able to read the classics of plant geography and the complete set of Engler's *Jahrbücher für Systematik und Pflanzengeographie*.

The greatest influence on the line EIG's work was to take has undoubtedly been exerted by the famous Professor N. I. VAVILOV, from Russia, who visited Palestine in 1925 to collect species and varieties of cereals and vegetables. He brought with him a complete list of systematic units which in his opinion—according to his theory of Homologous Rows—were bound to occur in Palestine and Syria. EIG accompanied VAVILOV during the few months he spent travelling in this country, and could convince himself that VAVILOV was right with many of his guesses. As he came to know him better EIG became, and remained until his death, the pupil and friend of this great scholar. The basic idea of VAVILOV and his school is that the Linnaean species accepted in systematic botany is composed of a number of autonomous systematic units of a lower order which correspond to different ecological habitats. The majority of wild relatives of the cultivated species grow in nature in habitats similar to those of the cultivated plants. The species *cylindricum* and *cras-sum* of the genus *Aegilops*, for example, which are closely related to soft wheat, grow under conditions resembling those under which this wheat is usually cultivated, while conversely the species *triunciale* of the same genus, which in a botanical and physiological

sense is a distant relative of soft wheat, also grows under ecological conditions widely different from those under which soft wheat thrives. EIG began therefore, under VAVILOV's influence, to study the ecological amplitude of plant species in Palestine. In addition, VAVILOV caused him to undertake a systematic study of the genus *Aegilops* (2). In this paper EIG particularly stressed the value of the ecologico-geographical conceptions of the Russian school. We wish to point out that before leaving for Russia and Germany to conclude his monograph on *Aegilops* EIG became acquainted with TURESSON's paper on the formation of oekotypes which was published in "Hereditas" in 1925.

Some time before, in 1925, EIG had become interested in the phytogeographical structure of the flora of Palestine, after reading our phytogeographical paper on the fungi of Egypt. In this paper an attempt was made for the first time to analyse the elements of a part of the Mediterranean flora. EIG then told us that it was his ambition once to carry out similar studies of the higher plants of Palestine. He was able to put this into practice when he came to Montpellier to work on his thesis for a doctor degree under PAVILLARD and BRAUN-BLANQUET. The last-named, in particular, gained a deciding influence on EIG's further development. It was BRAUN-BLANQUET who introduced EIG into the depth of phytogeographical problems and from whom he learned the exact methods and received the impulse to start plant sociological investigations of his own. When EIG returned from Montpellier in 1930 he was full of ideas and plans for the study of the vegetation of Palestine.

In the following chapters we shall analyse the phytogeographical problems on which EIG was engaged and stress his original contributions.

GENERAL CONCEPTIONS

Never before have the Mediterranean countries been the subject of a phytogeographical analysis as detailed as that made by EIG. He met with some difficulty in the use of phytogeographical terms which were mainly coined in connection with the vegetation of northern countries. He therefore had to clarify certain general conceptions which were at the time used in plant geography.

Region

The plants spread over the globe are divided by different authors in accordance with their view of the relative importance of the various factors concerned in the formation of the plant kingdom. ENGLER greatly emphasized the importance of geological and genetic processes for the formation of plants and divided the latter into territorial units after their distant geological past. GRISEBACH, on the other hand, only considered direct climatic influences and divided the plant kingdom into territorial units after the climatic conditions of their habitat. SZYMIEWICZ and EMBERGER also recently stressed the climate factor. BRAUN-BLANQUET used for the delimitation of his territorial units properties taken from the vegetation (climax society) and from taxonomy (in his paper on the element which was published in 1919, and in his book on the Sociology of Plants which appeared in 1928). EIG did not content himself with these two factors but added, or rather stressed, the ecological conditions as a third factor which exceeds the first-named two factors in importance (although it must be admitted that in BRAUN-BLANQUET's term "vegetation" the ecological factor is also indirectly implied). In his first paper of 1931 (3) EIG wrote that the phytogeographical regions "forment un ensemble naturel aussi bien au point de vue biológico-physiologique (expression des conditions écologiques qui prévalent aujourd'hui) qu'au point de vue floristique (héritage des époques antérieures)". Where taxonomic composition and ecological conditions do not agree with each other EIG preferred the ecological factor to decide. He wrote on page 99 of his book on the elements (3): "Entre les affinités systématique-historique qui engageraient à la fusion et la spécialisation écologique, qui milite en faveur de la séparation, nous choisissons l'écologie. Dans ces questions de délimitation et d'indépendance des régions naturelles, l'écologie nous paraît, à certain égards, l'emporter sur la systématique". In his second work on the question which was published in 1933 (7) he still more strongly emphasized the importance of ecological conditions. He wrote on page 471: "Historical facts of genetic relationship of sippes and plant groupings or of ancient expansion of certain floras can thus have no absolute value in the consideration of the delimitation of natural phytogeographical units". Elsewhere, on page 472, he wrote in the same paper (7): "One can define a phytogeographical region as

follows: stretches . . . possessing a more or less specialised and to a certain degree homogeneous flora and vegetation, which show a great biológico—physiognomic homogeneity, the expression of prevailing ecological conditions”.

For determining the properties of a phytogeographic region EIG therefore assigned first rank to the ecological conditions. The emphasis which EIG laid on ecology must no doubt be regarded as an attempt to create a synthesis between the conceptions of DRUDE and BRAUN-BLANQUET and those of GRISEBACH and EMBERGER. In his paper published in 1933 (7) EIG says himself on page 472: “In phytogeographical considerations we agree rather with GRISEBACH”. The weight EIG attached to ecological conditions represents an important advance in the modern tendency of phytogeography, headed by BRAUN-BLANQUET, to free areal phytogeography from the historic aspects stressed by ENGLER.

Element

The exact meaning of this important phytogeographical term has undergone many changes since CHRIST first used it in 1867. He divided all plants of the Alps into different groups with a common geographical distribution and genetic past and called these groups “elements”. In an excellent analysis of the term element, which she published in 1903, MARIE JEROSCH demonstrated different authors to employ this term in different senses. Apart from the two meanings, the geographical and the genetic, which CHRIST had given to it, the term was also used to cover a third and new meaning, viz. the common migration of plants. EIG’s contribution to the conception of element was that he added to it a fourth—ecological—meaning the lack of which had been very noticeable before. In his view the term element does not cover only geographical relationships and is not only applied to plants which happen to occupy the same area, as used by JEROSCH, but it has to be used in an ecological sense as well, to include plants linked with each other by common ecological habitats. EIG himself in 1931 (3, p. 10) defined this new meaning of the element as follows: “. . . les sippes et les groupements des végétaux spéciaux qui reflètent les conditions écologiques particulières, forment ensemble “l’élément” de chaque région”. In this definition EIG clearly follows BRAUN-BLANQUET who first used the term element to designate much

more than simply geographical distribution. In his classic paper on the element conception, which he published in 1919, BRAUN-BLANQUET for the first time defines it as follows: "L'élément phytogéographique est l'expression floristique et phytosociologique d'un territoire étendu défini". This definition by BRAUN-BLANQUET evidently by itself comprises to some extent the ecological principle, —(how can plant sociology be thought of without an ecological basis?)—much as this was also contained in his definition of a phytogeographical region; but here, the same as there, it was EIG who first emphasized the importance of just the ecological meaning of the term element. This was stressed in particular in the paper he published in 1933 (7, p. 472): ". . . the conception of phytogeographical element emphasizes the relation existing between flora and vegetation and ecological conditions". We regard EIG's emphasis on the ecological aspect in the definition of "element" as an important advance in floristic phytogeography. He revealed a new aspect of the distribution of plants, which many had felt to be lacking, but which nobody had formulated before him.

Plants of Connection

This phytogeographical conception was introduced by EIG (3). He meant it to denote plants growing in two neighbouring regions, under more or less similar ecological conditions. *Anemone coronaria*, for example, must be looked upon as a Mediterranean—Irano-Turanian plant of connection as it thrives under similar conditions in both regions. According to EIG such plants should not be called elements of both regions, as was customary until now, but Plants of Connection. The reason for his suggesting this name lies in his conception of the term element. In his opinion the "element" represents the phytogeographical incarnation of a region, and it cannot therefore comprise two regions at once. Earlier students who took the term element merely to cover geographical distribution could content themselves with the fact that an element was introduced or distributed over two geographical regions. EIG, however, who attached a narrow ecological meaning to the term element, had to coin a new name for ecological elements occurring in two different regions.

Pluriregional Plants

EIG gave this name to plants growing in various regions distant from each other (3). These plants had so far been called

cosmopolitan or ubiquitous elements, i. e. plants occurring in numerous localities. But EIG remains consequent and maintains that the term element which expresses the ecological composition of a region cannot be applied to plants which occur in many regions. EIG also showed that these plants do not appear anywhere, as had been previously assumed, but that they, too, are limited to definite edaphic conditions in respect of which the different regions resemble each other. He therefore called them pluriregional plants.

FLORISTIC PLANT GEOGRAPHY

Division of the Xerothermic Zone.

The xerothermic zone comprises all those areas of the Old World where the prevailing heat and drought have created a special xerophytic vegetation characterised by the outward appearance as well as the structure of the plants. This zone extends over Southern Europe, Northern Africa, and Anterior and Central Asia. Opinions differ up to this day on how this zone is to be divided into smaller phytogeographical units. BOISSIER, RIKLI, BRAUN-BLANQUET and others divide it into three parts: A Mediterranean Region comprising the countries bordering the Mediterranean Sea where sclerophyllous maqui has developed, and the regions of the steppe and the desert which extend from North Africa to Central Asia. On the other hand ENGLER, BACCARINI and other authors regard the countries of Anterior Asia with their steppes as belonging to the Mediterranean region. ENGLER unites the Sahara desert with the Palaeotropis. More recently ADAMOWICZ and MARKGRAF included the southern parts of Central Europe in the Mediterranean region. EIG reviewed all these opinions in the light of a floristic and especially ecological analysis of this zone; basing on GRISEBACH and BRAUN-BLANQUET he gave a new ecological definition of the regions it comprises. This definition bases on hydrothermic curves of the various types of climate, on edaphic conditions, on the kind of vegetation etc. All these criteria clearly bear out the fundamental differences between these three regions. In accordance with his division EIG also gave these regions new and distinct names (3): He called the maqui region Mediterranean, the steppe region Irano-Turanian, the desert region Saharo-Sindian, and the subtropical region (south of the Saharo-Sindian) he called Sudano-Deccanian. This division of the xerothermic zone

as proposed by EIG proved very useful indeed and is to-day accepted by the majority of phytogeographers. No one before him has ever defined these four regions so clearly.

Subdivision of the Xerothermic Regions

Great importance also attaches to EIG's subdivision of the above mentioned regions, which is based on a detailed floristic analysis (3). He subdivided, and again confirmed previous subdivisions of Southern Europe into a Western part including France and Italy, and an Eastern part including the Balcan Peninsula, Asia Minor, Syria, and Palestine. EIG's further division of North Africa was in contrast to the generally accepted view of DURAND and BARRATTE who joined Cyrenaica to the western part of the Mediterranean Sea (i. e. to Morocco and Algiers). EIG proved by means of a new floristic analysis that Cyrenaica belongs to the eastern part of the mediterranean countries, i. e. to Egypt and Palestine. Our lichenogeographical researches in North Africa (Bull. Soc. Bot. de France 83: 836, 1936, and Nuovo Giornale Bot. Ital., N. S., 44: 188, 1937) confirm this view of EIG's. We must, however, point out that the table lands (Hauts-plateaux) of North Africa, which EIG included in the Saharo-Sindian region (3), according to our above mentioned investigations belong to the steppe, or Irano-Turanian, region. But we also have to mention that EIG afterwards altered his opinion and agreed to our view, as he told us, on the strength of additional observations of the phanerogamous flora.

The Saharo-Sindian region was subdivided by EIG into three parts: a western part which comprises the West of North Africa as far as Libya, a central part which comprises Egypt, Southern Palestine, Northern Arabia, and Mèsopotamia, and an eastern part comprising the desert which extends from beyond Mèsopotamia up to the Sind desert in West India. The desert stretches of Cyrenaica thus belong, according to EIG, to the western part of North Africa. Here, too, we have to note that from a lichenogeographical point of view Cyrenaica would appear to us to belong to Egypt and Palestine rather than to Tunesia and Algiers, just as in the above mentioned case of the Mediterranean region.

EIG succeeded in furnishing conclusive evidence as to the floristic distinctness of the Saharo-Sindian from the Sudano-Dec-

canian region. It must not be overlooked that many scholars, from ENGLER to MAIRE, the greatest phytogeographer of North Africa, did not distinguish properly between the plants of these two regions. This is due to the fact that these regions somewhat resemble each other in climate and soil conditions and, before all, because the plants of one region frequently appear in the other region. In keeping these two elements apart EIG showed himself as a master of ecological distinction. He was the first to point out that this intermixture of two elements only occurs under very special conditions in the absence of which each element remains by itself and in its region. The Sudano-Deccanian element, for example, always occurs in the Saharo-Sindian region under special conditions of excessive soil-moisture and in the absence of salt-accumulation. Under the normal conditions prevailing in the Saharo-Sindian region the Sudano-Deccanian element is unable to survive there.

Palestine

The greatest achievement which EIG has left to future generations is undoubtedly his phytogeographical analysis of the plants of Palestine. TRISTRAM, HART, and others had previously stated that various phytogeographical regions met in Palestine. As regards the Mediterranean region this was evidently situated along the coastal plain. We also knew subtropical genera of plants to occur in the oases of the Jordan valley. But we knew nothing about the limits of the steppe and desert plants occurring in this country. When writing his first phytogeographical paper on Palestine in 1927 (1) EIG himself was unable to define the boundaries of the distribution areas of these plant genera on the map attached to the paper. He gave a common name—area of steppe and desert—to all the areas where these plants occur, i. e. to the greatest part of Palestine. It was only after three years' incessant travelling up and down the country that he permitted himself in 1930 to publish a new phytogeographical map (3), which marks a great advance in Palestinian phytogeography. Here we find clear indications of the boundaries of the different regions, the Mediterranean, Irano-Turanian, and Saharo-Sindian. But EIG did not content himself with this map which still contained many questions-marks, and continued to travel throughout the length and breadth of the country, to study the floristic composition of the vegetation. Of greatest importance were his systematic studies of

doubtful genera (*Astragalus*, *Anthemis*, *Erodium* etc.). EIG thus created the exact floristic basis for the areogeographic subdivision of Palestine. To characterize different regions he used the occurrence of certain sections of some genera in one of the regions. The section *Plumosa* of the genus *Erodium*, for instance, of which the centre of distribution lies in the Mediterranean, is typical of the Saharo-Sindian region. EIG devoted seven years to this work and in 1938, a few months before his death, he completed the revision of the phytogeographical map of Palestine (13). A comparison of this map with the one published in 1931 (3) clearly illustrates the great progress which EIG made in those seven years. On the earlier map the Beersheba-Gaza district was included in the Saharo-Sindian region, while on the new map it belongs to the Irano-Turanian region. The strip running from South of Hebron along the East of the Judean and Samarian mountains had from the outset been included by EIG in the Irano-Turanian region; but on the first map this strip only extended to north of Nablus whereas on the 1938 map it reached further north until south of the Huleh Sea.

The difference between the earlier and the later map is still more marked where Transjordan is concerned. On the first map the Mediterranean region extended to south of Kerak, which is on a line with the southern end of the Dead Sea, while on the last map this region does not exceed the northern end of the Dead Sea and all the area further south (including Kerak) is included in the Irano-Turanian region.

Never before have the different elements of Palestinian flora become as real from a climatic, edaphic, physiognomical and floristic point of view, as EIG rendered them by his work. The value of EIG's phytogeographical definitions is still added to, if it is remembered that they are based not only on investigations on the spot but also on comparison with corresponding elements in the countries bordering on Palestine, such as Iraq, Turkey, and Syria, where these elements have been better preserved in nature. EIG succeeded in these seven years to obtain results which elsewhere would represent the work of two generations.

Special mention must be made of EIG's study of the enclaves formed by certain elements outside their own region (3). Thus he

discovered in the coastal plain Saharo-Sindian and Sudano-Deccanian enclaves, the plant associations of which are headed by *Retama retam* in the former, and by *Eragrostis bipinnata* in the latter case. AARON AARONSOHN (Bull. Soc. Bot. de France 60: p. 495, 1913) has first drawn the attention of geobotanists to the fact that *Acacia albida*, a representative of subtropical flora, occurred near the coast; but EIG went right to the bottom of the problem by making the components of this and of other enclaves the subject of detailed study from an ecological, edaphic, phytosociological and genetic point of view.

Syria

EIG travelled to the countries bordering on Palestine in order to study there the natural formation of East Mediterranean flora and to gain in this way information on the flora of Palestine which in the course of time has suffered from human interference. Several times he went to Syria and South Turkey. One of his journeys which lasted 31 days was devoted to the study of the flora in the Lebanon, Amanus, and Taurus. He collected plants on the mountain-slopes and on their peaks at altitudes of up to 3000 metres. Under his influence the French Agricultural Inspector of the Alexandrette district, M. P. DELBES, published a floristic paper on the Amanus mountains (Bul. Soc. Bot. de France 84: 414, 1937). From the time that KORSCHY and POST visited these mountains, EIG was the first to study their flora seriously, and he penetrated to where no other botanist had been before. The majority of his observations and records has not yet been published; but a short paper on Syria appeared in a Hebrew Journal and described briefly the forests and tragacantic vegetation of the Amanus, Hermon, and Lebanon (5). The rich material EIG collected there still has to be exploited.

Iraq

EIG twice travelled to Iraq by way of the Syrian desert. His intention was to get acquainted with the desert-like steppe which lies between Palestine and Iraq, and to compare it with the desert proper in Iraq. The phytogeography of all these areas was entirely unknown. His second journey was undertaken at the invitation of the Iraqi Government which asked him to investigate the problem of locusts and their breeding places and to study the forests of Kur-

distan. EIG traversed the length and breadth of the country, the first time in the course of 40 days, and the second time in 30 days from the southern part bordering on the desert up to the mountains of Kurdistan in the north. Wherever he went EIG collected thousands of plants and made phytogeographical "relevés". He was particularly interested in the phytogeographical differences between steppe and desert. At his second visit to the Kurdistan mountains EIG went there at the head of a special expedition to study the forests and to make suggestions for the afforestation of these denuded mountain-sides. EIG thoroughly investigated this problem of afforestation and the climax forms of these mountains as compared with those of the Syrian and Palestinian mountains. Almost the whole of the material he collected is still unpublished and has yet to be examined. In connection with his report on the locust EIG gave a phytogeographical description of the entire region (11). He defined the exact boundaries of the Irano-Turanian and Saharo-Sindian regions and briefly reviewed the plant formations he had found there. In this short paper we are given a phytogeographical picture of the whole of Iraq. When his assistants will publish the material EIG collected we shall see how much he achieved on these short excursions.

GENETIC PLANT GEOGRAPHY

At various points in his papers EIG goes into the history of the elements of the Palestinian and North African flora. In his opinion, which is supported by the investigations of geological experts in Palestine and North Africa, the flora of these two areas has passed an identical development. The wide differences between their present flora only began to develop at the end of the second Pluvial epoch, when the climate prevailing in the Mediterranean was similar to to-day's climate, but moister and with higher precipitations. The Borealic element then invaded Palestine and North Africa from the north, and the Sudano-Decanian element from the south. The latter spread in two directions: into the Jordan Valley where it produced the enclaves along the Dead Sea with plants like *Balanites*, *Salvadora*, *Acacia* etc., and along the coastal plain where it gave rise to an important enclave with *Eragrostis bipinnata* and *Zizyphus Spina-Christi*. According to EIG elements from three different sources united in the coastal plain: the Sudano-Decanian element mentioned above

was the first and oldest; the second was the element of the north-eastern Mediterranean exemplified by *Quercus ithaburensis* which arrived when the climate had become somewhat drier; and the third element, which invaded the coastal plain and still continues to do so to-day, was by the Saharo-Sindian element, which came by way of the sands of the Sinai Peninsula and the Negeb when the climate became still drier, such as it is at present.

EIG used phytogeographical, or rather ecological, principles in solving problems of genetics and history in plant taxonomy. In his view the section *Pleionanthera* of the genus *Aegilops* developed earlier than the section *Macranthera*, as the former has a much wider area of distribution than the latter (2). Again, in his opinion in the genus *Erodium* the section *Plumosa*, which occurs in the Saharo-Sindian region only, is much younger than the section *Barbata* which is spread over the Mediterranean region. The former is of very limited systematic and ecological amplitude and grows on heavy soils only, while the latter possesses considerable systematic variability and a wide ecological amplitude, and also grows on light soils (14). Such genetical considerations basing on phytogeographical distribution are frequently met with in EIG's work.

ECOLOGICAL PLANT GEOGRAPHY

No systematic botanist before EIG has ever been so consistent in his application of ecological aspects to the solution of taxonomic problems. RICHARD WETTSTEIN in 1898 first introduced phytogeographical principles into systematic botany, and proved by his classic monograph on the genus *Gentiana* that the geographical distribution of species may be a clue to their systematic relationship and their territorial origin. But EIG was the first to be consequent in the use of ecologico-geographical conceptions for the purpose of defining the taxonomic relation between the species, or groups of species, within a genus.

With him differences in the growing conditions of plants decided upon the creation of new systematic units even where morphological distinctions were not so obvious. What TURESSON did on a small area and for systematic units of a lower order, and what VAVILOV and his school did for crop plants, was done by EIG in respect

of the distribution of plants over the regions of the world and for higher systematic units. It may suffice to recall the genera *Astragalus* and *Erodium* where he created numerous new species and variations distinguished chiefly by the fact that they occur under distinct climatic or soil conditions (4, 10).

With the help of ecology EIG explained the important and little understood phytogeographical phenomenon of the existence of forests, or their remnants, in the west of the Mediterranean part of the Samarian mountains but not in their East. He proved that in the West the soil is composed of layers of Cenoman which hold the moisture of rain waters and thus create conditions favourable to forest growth, while in the East of the Samarian mountains the soil consists of Senon layers which allow the water to drain off and thus preclude all possibility of forest development (6).

EIG found a similarly convincing explanation for the occurrence of Sudano-Deccanian enclaves east, but not west, of the Dead Sea. The reason is purely edaphic: East of the Dead Sea the soil consists of Nubian sandstone whereas in the West it is calcareous (3). The former conserves moisture, but the latter does not and consequently will not permit the development of Sudano-Deccanian flora which requires very humid conditions.

Soil conditions, i. e. heavy soil and the presence of ground water at certain localities, are further held by EIG to explain why the Sudano-Deccanian enclave, which is so dependant on humidity, persists in the coastal plain until to-day, although conditions there have become so much drier since the Pluvial epoch (3, 14).

EIG applied phytogeographical-ecological principles to the elucidation of phenological phenomena of the Palestine flora. In the neighbourhood of Tel-Aviv and Jaffa, which lie in the Saharo-Sindian enclave, perennial plants continue to flower even in late summer when plants in other parts of the coast north of Tel Aviv have ceased to flower for a long time. This is due to the fact that Saharo-Sindian perennials also use to flower later in the desert (3).

In connection with his ecological observations on the distribution of plants EIG made an interesting phytogeographical discovery. The plants typical of the Western Mediterranean are well-known

to love moisture and therefore become less and less frequent as we advance towards the Eastern Mediterranean. In Palestine EIG met with only a few plants characteristic of the Western Mediterranean, such as *Coronilla repanda*, *Lupinus reticulatus* and others; and all of these were found in the coastal plain, and without exception in sandy clay soils poor in chalk, i. e. in soils conserving a maximum of moisture (14).

SOCIOLOGICAL PLANT GEOGRAPHY

EIG only approached plant sociological research in the last years of his life, when he had more or less accounted for the floristic, geographical and ecological composition of Palestinian plants, and after he had travelled to the countries neighbouring Palestine. There he found the phytogeographical regions met with in Palestine developing naturally and without the interference of man. Together with his assistants EIG recorded thousands of floristic relevés of the various plant associations in Palestine, Syria, Southern Turkey, and Iraq, in forest regions, on the heights of alpine mountains, in the desert and the steppe. The material collected still requires many years of careful study. Almost nothing has so far been published of the plants collected in the neighbour countries, with the exception of two short papers on Iraq and Syria (5, 11).

EIG nevertheless succeeded in completing two important plant sociological papers on Palestine: the first on the development of *Quercus ithaburensis* in Palestine (6), and the second on the flora of the light soils of the coastal plain (14). In the former paper, published in 1933, EIG treated the problem of the climax of the Mediterranean region in other countries and in Palestine itself. He discussed the different opinions on the form this climax may assume, and whether in localities where maqui occurs this represents the climax or only a degredate type of it. After prolonged search and intensive study EIG found that in Palestine, too, the climax is constituted by forest, and that on high mountains *Pinus halepensis* forests represent the most advanced type of vegetation. All along the coastal plain from Acre to south of the Yarkon river, in Upper Galilee, in part of the Yesreel Valley, and in Gil'ad in Transjordan, Palestine had been covered by forests of *Quercus ithaburensis*. EIG presented lists of the plants growing in association with the rem-

nants of these forests and thus reconstructed the forest flora of Palestine. We must admire the way in which EIG in this paper used for the purpose of his research not only phytogeographical findings but also data hidden and dispersed in earlier literature and in travelling accounts of various tourists of earlier or more recent times.

As stated above, EIG was still able to work out from his sociological records a description of the plant associations found on the light soils of the coastal plain; this work will soon be published in extenso, but only a preliminary paper has hitherto appeared (14). But even this suffices to show how profoundly EIG grasped the different problems of plant associations and their development. On light soils EIG distinguished three habitats: the coast proper, the recently formed dune system, and the old calcareous dune system. In each habitat there has formed an alliance with three special plant associations. The first alliance is typified by *Lotion cretici*, the second by *Artemision monospermae*, and the third by *Eragrostion bipinnatae*. EIG gives a detailed description of the ecological conditions under which such alliances form and outlines the history of these alliances as well as the succession of their development which we have noted above.

Apart from these two phytosociological papers it was not given to EIG to exploit the wealth of his material in this line of research. His aim was to compile a phytosociological map first of Palestine, and later of the neighbouring countries.

APPLIED PLANT GEOGRAPHY

Although EIG by his systematic and phytogeographical researches penetrated far into the problems of pure botany, he nevertheless always remained faithful to his first teacher N. I. VAVILOV who had taught him to use the methods of pure botany for practical purposes. With all his botanical researches in Palestine EIG never lost sight of the practical ends. In a lecture to the Palestine Agronomists' Association (12) he once outlined how closely his line of research was ultimately connected with practical problems. He believed that phytogeography, especially in its ecological aspect, revealed new possibilities to practical agriculturists all the world over, but particularly to the young Palestinian agriculture which is being developed

by Jewish colonization. The plants, and especially the plant associations, may be used as indicators of climate and soil-type, and colonization can be directed in accordance with them.

EIG believed that on the basis of investigations of the climax forms of Palestinian forests new ways and means had been discovered for the afforestation of Palestine's mountainsides with its various soils and conditions. He also worked out special programmes and memoranda for this purpose. As mentioned above he was invited by the Iraqi Government to study the forests of Kurdistan, and as the result of his investigations he proposed a detailed afforestation scheme.

In EIG's view many wild plants with economic properties could be introduced into cultivation by VAVILOV's method. It was in this connection that he closely studied the taxonomy and geographical distribution of the species of clover (9).

On the basis of his phytogeographical and phenological research EIG worked out a big scheme for the use of the plants of the wild flora as honey flowers (8).

EIG further used the results of his phytogeographical investigations to discover ways and means of combating the locust which is a permanent resident of Iraq and from time to time spreads from there to the countries of Anterior Asia. UVAROV, BODENHEIMER, and other investigators of the locust had established the fact that its appearance is conditioned by a definite set of climatic conditions. But in view of the fact that no meteorological data were kept in the countries where locusts occur it proved difficult to determine the exact influence of the environment on the appearance of locusts. EIG suggested to use the vegetation as a climatic and ecological indicator which marks the exact conditions under which locusts appear (11). He found that locusts only deposit their eggs in the Irano-Turanian, but never in the Saharo-Sindian region of Iraq. He also described the plant associations which they prefer for egg-laying. The significance of this knowledge for all countries of the East will be readily appreciated.

* * *

This briefly summarizes EIG's phytogeographical work in the course of fourteen years. At the beginning of his work the plants of Palestine were far from well explored; at his death he left us a

more or less critical flora, a phytogeographical map, the bulk of the material required for the compilation of a phytosociological map of the country, and material for important contributions to the knowledge of the vegetation of Syria, Iraq and Southern Turkey. The important researches he has published have largely contributed to the clarification of the fundamentals of plant geography. Most of his work has not yet been summed up. It is the duty of his pupils and assistants to publish it for the benefit of botanical science in general and in particular of Palestinian botany which has suffered so cruel a loss by ALEXANDER EIG'S untimely death, and which will never cease to remember him.

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ORANGE LEAF TRANSPIRATION UNDER ORCHARD CONDITIONS

PART I: SOIL MOISTURE CONTENT HIGH 1)

A bioclimatic study

By H. R. OPPENHEIMER AND K. MENDEL,

(Division of Horticultural Physiology and Genetics,
J. A. f. P. Agr. Res. Sta., Rehovot).

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1) Part II: "Soil moisture content decreasing" will follow.

A. INTRODUCTION.

Though several authors have studied citrus leaf transpiration, no studies of an ecological nature, based upon reliable methods exist. At present little is known of the natural daily and yearly march of transpiration in the grove. Until this gap in our knowledge is filled, it seems impossible to approach the solution of the problem of an economical use of irrigation water in the citrus grove from a biological point of view.

Studies of the use of irrigation water are generally based upon determinations of soil moisture rather than upon the needs of the plant. Soil moisture, however, is influenced not only by water absorption of the roots, but also by percolation and soil evaporation, and gives insufficient information on the use of water by the trees. Therefore, physiological studies must be added to soil moisture and wilting-point determinations if a real understanding of the effects of irrigation on the trees is desired.

In 1934, the present writers published a short study on the water relations of citrus trees (53) in which an approximate picture of the daily march of the transpiration of nursery trees under field conditions, based on the coloration of standardized cobalt chloride paper, was given. A grant of the Palestine Government enabled the continuation of this research with more adequate and reliable methods.

The main objects of this study were (1) the determination of the daily water losses of Jaffa orange leaves in the grove by hourly measurements taken from dawn to after sunset; (2) the determination of the changes in these daily losses in the course of the year; (3) the dependance of the changes in the transpiration rate upon (a) meteorological factors and (b) regulations by the plant. The investigation, as far as its results are published in this report, was restricted to the water loss under conditions of sufficient soil moisture.

B. TREES AND SOIL.

For the measurements, six year old Jaffa orange trees were chosen. These trees, budded on Sweet Lime stock, grew in a young experimental grove of the Agricultural Research Station at Rehovot. The trees were of uniform size. The stocks had been sown in winter 1928/29, budded in November, 1930, and the trees transplanted to their present location in spring, 1932.

One tree dug up in spring, 1935, was weighed and measured. The results of these measurements were: roots—2.880 Kg., trunk—2.700 Kg., branches—3.120 Kg., leaves—5.350 Kg., diameter of the trunk at base 7.0 cm. and above the bud-union 6.1 cm. The trunk was 80 cm. high and the whole tree was about 2.50 meters in height. The total number of leaves was 3,436 and the average weight of a single leaf was found to be 1.556 g.

One of the trees which served for the first measurements in October and November, 1934, was found to bear nearly 4,000 leaves. The trees blossomed in spring, 1935 and yielded some fruits in autumn.

The soil was composed of a rather fine uniform alluvial sand reaching to a depth of one to two meters, underlaid by a heavier layer of red loamy sand ("khamra"). The soil was kept near field capacity by frequent irrigations, applied during the whole summer at intervals of about two weeks.

The moisture content of the sand was determined at the time of the first (October) measurement. It amounted to only 3.6% at a depth of 30 cm. and to 3.5% at a depth of 70 cm. It was found impossible to measure the suction tension of this soil with the HANSEN-GRADMANN (26) method at this moisture content, as condensation of water on the inner walls of the bottles containing the soil samples could not be prevented. GRADMANN (26a) recently showed, that, by using his method, measurements of very low suction tensions require a remarkable degree of thermostability so that fluctuations of temperature do not exceed 0.1°C. Thermostates of this degree of accuracy were not available in our laboratory. As even hygrometers impregnated with a 0.05 M. NaCl solution showed a considerable increase in weight, when hung in bottles containing these soil samples, it may be assumed that the water in this case (which is typical for the amount of moisture prevailing in the soil during the whole of our investigation) was bound to the soil by surface "forces" not exceeding one to two atmospheres, i. e. was indeed "readily available", in the sense of BOUYOUKOS (14).

In order to determine the suction force of the Sweet Lime root, the osmotic pressure of the absorbing rootlets was measured. 0.25 M. cane sugar solution (corresponding to an osmotic pressure of 6.4 atmospheres) was found to cause limiting plasmolysis of the

cortex cells, while 0.20 M. (5.1 atm.) proved sufficient for the plasmosis of the cells surrounding the internal vascular bundle. The absorptive activity of the roots should, therefore, not be paralysed before the suction tension of the soil reaches, at least, five atmospheres.

C. FACTORS GOVERNING TRANSPIRATION.

I. *External factors.*

1) *Climate of Rehovot.*

The Agricultural Research Station of Rehovot is situated in the coastal plain of southern Palestine, about 20 Km. SSE of Tel-Aviv, at 31°55' N, and at 34°48' E of Greenwich. The distance from the Mediterranean Sea is about 10 km. The buildings of the Station are located on a hill, 58 meters above sea level. Rehovot is a centre of the southern citrus belt of Palestine.

Temperature.

January is the coldest month, with an average temperature of 11.9°C. August is the warmest month having a mean temperature of 25.2°C. Comparing these figures with those of other regions of citriculture, we find:

Region	Coldest month	Warmest month	Difference
Rehovot	11.9°	25.2°	13.3°
Riverside (Cal.) (1)	10.0°	24.5°	14.5°
Santa Barbara (Cal.) (1)	12.5°	19.0°	6.5°
Bartow, Polk Cty. (Fla.) (2)	15.5°	27.8°	12.3°
Catania (Sicily) (3)	10.5°	27.1°	16.6°
Grahamstown (S. Afr.) (5)	12.7°	21.6°	8.9°
Sao Paulo (Brazil) (3)	14.3°	21.0°	6.7°
Castellon (Spain) (4)	9.9°	24.8°	14.9°

(1) Forbes, S. and Young, A. A., Irrigation requirements of the arid and semiarid lands of the Pacific Slope basins, U.S.D.Agr. Techn. Bull. No. 379, 1933.

(2) Swinson, C. R. and Funk, W. C., Economic aspects of citrus-fruit growing in Polk Country, Fla., U.S.D.Agr. Dept. Bull. No. 1435, 1926.

(3) World Weather Records, Smithsonian Miscellaneous Collections, Vol. 90, 1934.

(4) E. A. Martinez, La Agricultura y el Clima, Barcelona, 1932.

(5) Southern East Africa Yearbook and Guide for 1937, London.

The yearly march of temperature at Rehovot, as compared with that of other regions of citriculture is represented in fig. 1.

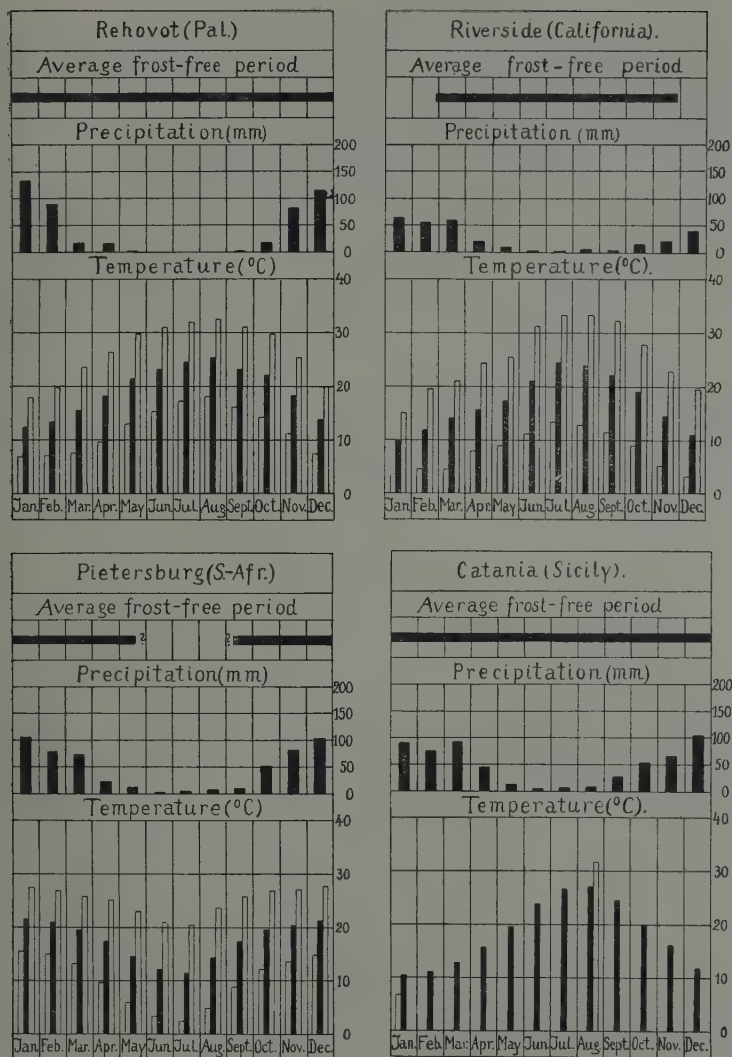


Fig. 1.

Condensed climatology of four places in important Citrus belts of the world, showing average frost free period, mean monthly precipitation and average mean (black column), minimum (left white column) and maximum (right white column) temperature.

Records taken from the mentioned literature and de Philippis, A., *Classificazioni ed indici del clima in rapporto alla vegetazione forestale italiana*. Firenze, 1937.

The absolute maximum temperatures of the year are not reached in the course of the midsummer months, but during the periods of hot desert winds, locally known as "sharav" or "khamsins" which blow in spring and in autumn. In most cases the absolute maximum of the year is found during a spring khamsin, and only rarely is it reached in the autumn, as happened in 1937, when the yearly maximum was recorded in October. The absolute maximum of the last five years was reached at the Research Station on June 13th, 1933 at 14:00, when the temperature rose as high as 42.2°C. in the shade. Temperatures of about 40°C. are, in any case, reached every year in khamsin periods.

Usually the absolute minima are recorded in the months of January or February, and less frequently, in December. They seldom sink below 0°C. Frosts injurious to citrus crops or even to citrus trees are of rare occurrence, appearing at intervals of many years.

Humidity.

Bright rainless winter days are characterized by a steep fall in the relative humidity of the air in the morning hours followed, in the afternoon, by a similarly steep ascent. On such days, humidity sinks from about 100% (heavy dew is typical for these nights) to less than 50%, rising at about 18:00 or 19:00 again as high as 85 or 90%. It is well known that at low temperatures and at a consequently low water content of the air, a small rise in temperature is sufficient to provoke a considerable decrease in humidity. In the summer months, which are characterized by high moisture of the air, the humidity rarely sinks below 60%, as a consequence of western marine winds. Conditions are quite different during the khamsins and during the periods of cold east and north east winds, which prevail in winter (Kadim; Sharkiya). At such times humidity sinks to a low level, usually rising in the night not higher than 60%. During the day it may sink even below 10%. The absolute minimum of humidity during the last five years was recorded on May 2nd, 1935, at 11:00, when it sank to 6%.

Evaporation.

Regular observations on evaporation at Rehovot were started only recently. So far, evaporation was found to be very low during the winter, rising considerably between spring and early summer, and

sinking again in late summer. On scirocco days the evaporation is sometimes three times greater than on ordinary days.

The following table, showing measurements carried out in 1937, illustrates the intensity of evaporation during the dry summer months, from March to October, which coincide roughly with the period of irrigation.

TABLE I.

Evaporation intensity in millimeters per 24 hours (Piche tube) measured at the Rehovot Agricultural Research Station, from March to October 1937.

Month	Average	Maximum	Minimum	Number of Khamsin days
March	4.3	8.4	3.9	5
April	7.5	>21.2	3.3	11
May	6.7	14.2	3.7	6
June	6.7	8.1	4.7	0
July	5.9	8.4	4.9	0
August	6.2	7.6	4.1	0
September	6.1	8.0	3.6	0
October	7.1	15.2	3.2	10

Winds.

Summer months in Palestine are characterized by very regular local winds. At night a slight east or southeast wind blows from the continent. This wind subsides in the early hours after sunrise. An hour of calm, between 7:00 and 8:00, follows. A little later, a slight breeze from the west sets in, blowing with increasing intensity (2—3; *Beaufort*) until the afternoon, when it gradually slackens. From 18:00 or a little later, a second calm is observed, followed by the above mentioned continental wind starting between 20:00 and 21:00.

During the other seasons, wind conditions and weather, in general, are much more unstable. SE to E winds blow during khamsins, and NE to E winds during sharkyas. At the beginning of the rainy season the rain-bearing winds are S to SW; in mid-winter, W; and at the end of the season frequently W and NW. (cf. ASHBEL).

The number of khamsins and sharkya days at Rehovot is much lower than at Jerusalem, where ASHBEL recorded about 170 such days per annum. In Rehovot, we recorded an average of 57 such days annually during the last five years (1933—1937).

Precipitation.

According to ASHBEL's (3) map of the rain distribution in Palestine, the total amount of precipitation per annum ranges at Rehovot between 550 and 600 millimeters. At the Rehovot Station about 450 millimeters were established as an average for the last five years, three of which had, indeed, a very scanty rainfall. The average monthly distribution of precipitation for the last five years was as follows:

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
133.5	90.5	15.9	16.2	1.1	0	0	0	1.4	17.2	81.5	114.0

Owing to this distribution of rains the irrigation period at Rehovot generally starts in the middle of April and ends in October.

2) *Site and microclimatical conditions.*

The transpiration measurements were carried out at a distance of about 180 m. west of the station buildings, close to the main Jaffa-Gaza road, a place about 15—20 m. lower than the buildings. This area is protected from S and W winds by a row of Casuarina trees, eight meters high. A nearby forest of Eucalyptus trees, also serves as a windbreak. The area is open on the NW, N and NE sides, where the ground slopes lower. A young orchard extends east — and south-eastwards.

Owing to these local conditions, the temperature generally rises somewhat higher (1—2°C) in the warm hours and the humidity of the air sinks somewhat lower (5—10%) than at the meteorological station situated on the top of the hill. The strength of the west winds is diminished and about one hour and a half before sunset, the observed orange trees are shaded by the Casuarina windbreak.

3) *Meteorological measurements.*

Concomitantly with the transpiration experiments, measurements of the following factors were carried out: light intensity, estimated overcasting of the sun, cloudiness, temperature of the air and soil, relative humidity of the air, wind velocity and evaporation intensity of the atmosphere.

As the meteorological equipment of our laboratory was rather poor at the time when the investigation was started, we were obliged to use primitive methods in most of these measurements.

a) *Light intensity.* The light intensity, or more correctly, the vertical component of the radiation of the sun and sky, was measured by an Eder-Hecht gray wedge photometer. This instrument, measuring in particular the blue light radiation, was exposed horizontally on the soil or on a table, in an open place, every hour for five minutes. It was directed so that its long axis

was towards the sun. According to the varying conditions of the seasons, wedges with the constants 0.305 (in summer) and 0.188 (in winter) were chosen. The readings were taken immediately after exposition, in a dark room in the neighbourhood, where the photometric papers, standardized according to the instructions of the *Davos Meteorological Institute*, were changed. No fixative was used before the readings. Relative values of light intensity corresponding to the readings were obtained from tables.

By this method, maximum relative light intensities ranging between 127 and 180 rel. units per five minutes were found between September 23rd and March 5th. In the period from March 19th to August 21st, the energy of radiation, as far as it can be determined by the above instrument, ranged between 207 and 283 rel. units per five minutes: that is, it was by far higher than during the aforementioned winter period. It may be added that the gray wedge photometers were found unreliable on hot sunny days in Palestine. Apparently the jelly layer on the photometric papers is liable to undergo changes under the influence of the heat and give rise to incorrect figures.*)

b) *Sunshine and Cloudiness*. As no self-registering instruments for sunshine measurement or actinometers were at our disposal at that time, we were obliged to estimate degrees of overcasting of the sun in the usual way, making use of the symbols S_0 to S_8 , " S_0 ", meaning that the sun is uncovered and " S_8 " signifying that it is invisible. In view of the fact that the direct radiation of the sun is a factor of very great importance in the transpiration of plants, we are glad to state that this primitive method rendered very useful services. Cloudiness was estimated in the usual meteorological manner (using the index numbers 0—10 to estimate the various degrees of overcasting). A separate note was made of the presence of haze.

c) *Temperature and relative humidity*. Temperature and relative humidity of the air were measured by wet and dry bulb thermometers. Our instrument was of the whirling type, with thermometers tested by the *Physikal. Reichsanstalt* at Berlin. In our diagrams we registered instead of the relative humidity (H), the values of percentage saturation deficit ($100-H$), as under conditions of sufficient soil moisture the former stands in an inverse and the latter in a direct relationship to the intensity of evaporation and transpiration.

The temperature of the air, observed during these measurements, fluctuated between $+5$ and $+36.2^\circ\text{C}$. On May 20th, the khamsin day mentioned above, the temperature rose very quickly. At 4:30 it was 16.4°C and a maximum of 36.2°C was reached at 11:00. These values mark the widest fluctuations observed in the course of our measurements. Fluctuations of about 15 degrees between sunrise and the daily maximum were frequently found.

The relative humidity of the air between dawn and sunset fluctuated within relatively wide limits. The fluctuation was found to be relatively small on

*) Oral communication by Dr. D. ASHBEL, of the Meteorological Institute of the Hebrew University.

cloudy winter days (20.II.) and very great on clear winter days. On December 18th and January 21st it was more than 50%. The fluctuations amounted to 50% in April, reaching their maximum of 63% in May (khamsin day) and again falling to about 46% from June to October, under the steady conditions of the Palestinian summer.

Table No. II gives further information about these fluctuations.

TABLE II.

The amplitude and limits of fluctuations of humidity (%), the drop of relative humidity during the first three hours after sunrise and the ascent during the last three hours before sunset.

Date	Oct. 18th	Nov. 21st	Dec. 18th	January 21st	Febr. 20th	March 5th	March 19th	April 21st	May 20th	June 20th	July 18th	August 24th	Sept. 23rd
Max. fluctuation	40	40	52	57	30	44	45	50	63	44	38	29	35
Limits	92 52	78 38	85 33	93 36	80 50	96 52	79 34	83 33	87 24	90 46	81 43	86 57	87 52
First 3 hours drop	31	21	45	44	13	28	12	33	35	24	16	15	17
Last 3 hours rise	15	28	15	12	?	14	16	16	3	20	27	5	9

It is to be noted that khamsin days (20/V) and dry winter days (18/XII and 21/I) are characterized not only by wide fluctuations of humidity, but also by a very steep drop in humidity in the first three hours after dawn. In addition it is to be remarked that the rise of humidity in the evening proceeds, in general, at a much slower rate than the drop in the morning. The relatively mild conditions of the late summer (VII—IX), with increased cloudiness at sunrise and consequently weakened radiation of the sun, are reflected in the less marked changes in humidity in the morning as compared with the early summer conditions (IV—V).

d) Soil Temperature. Soil temperature is a factor of the utmost importance for the water balance of the trees. We took measurements at depths of 25, 50, 75 and 100 centimeters. During our first measurements in October and November, 1934, we made use of good instruments, specially manufactured for this purpose, which were placed at our disposal through the courtesy of the Department of Agricultural Chemistry of our Station. Later we were obliged to use common thermometers for these measurements. Every three hours, a narrow, vertical hole was dug in the ground with a spade and the thermometer quickly inserted into one of its lateral walls at the desired depth. By deepening the hole after each measurement, we arrived at the new depth of measurement only immediately before the insertion of the instrument, thus avoiding any

appreciable change of temperature. In this way, of course, slightly inaccurate measurements were obtained. We feel certain, however, that the error rarely exceeded 0.5° , probably reaching 1°C. at times, which degree of accuracy was sufficient for our purposes.

Towards the end of the year of our measurements, we received a new set of soil thermometers in brass sheaths. These, however, could be used only during the last measurements in September, 1935.

Occasionally surface temperatures were measured. The maximum value recorded for such a measurement was 55°C. in the dry sand exposed to the sun, on July 18th, 1935, at 12 o'clock. This value is not surprisingly high if we consider that HUBER (40) recently published measurements of soil surface temperatures exceeding 70°C. from the Elbe Sandstone Mountains in Germany, and that temperatures approaching this value were measured in midsummer even farther north, at the ecological station of Hiddensee, in the Baltic Sea at $54^{\circ}30' \text{ N.}$ These temperatures, however were recorded on southern slopes, exposed at a right angle to the rays of the sun, whereas we made our measurements on a horizontal plane. At any rate, the fact that soil surface temperatures in Palestine as measured by OPPENHEIMER (52), PERLBERGER (55), EVENARI and RICHTER (22) and the present authors (53) do not exceed maximum values measured in Germany again proves that microclimatical factors such as exposition are often more important in producing extreme conditions for vegetable and animal life than very great differences in the geographical latitude.

Table III contains the average daily values of soil temperature. The figures found at depths of 50 cm. and lower can be considered as quite accurate, as fluctuations at these depths during the day were, in general, smaller than 1°C. The figures found 25 cm. below the surface of the soil seem to be less reliable, since daily fluctuations of several degrees were found which probably do not correspond to natural conditions and must be accounted for by our primitive method of measuring. Nevertheless, the mean values, even at this depth, are probably sufficient for a biological study.

TABLE III.

Average daily soil temperatures ($^{\circ}\text{C.}$) measured in an open place in an orange grove at Rehovot, from October, 1934 to September, 1935.

Date	Oct. 18th	Nov. 21st	Dec. 18th	Jan. 21st	Febr. 20th	March 5th	March 19th	April 21st	May 20th	June 30th	July 18th	Aug. 21st	Sept. 23rd
Depth (cm.)													
25	25.5	18.2	14.8	13.1	(14.3)	19.4	22.6	21.8	26.4	29.3	30.9	28.6	27.4
50	25.7	19.2	16.2	13.7	(15.1)	19.0	21.0	20.4	25.1	28.2	30.3	29.0	27.5
75	26.5	20.9	17.4	14.8	(15.9)	19.1	20.8	20.3	(24.7)	28.2	29.8	29.2	28.0
100	27.3	22.9	18.3	15.7	(17.0)	19.2	20.6	20.8	24.3	27.6	29.1	(29.0)	27.9

NOTE: Values in brackets are based upon incomplete series of less than five measurements per day.

In table III we find that at depths ranging from 50 to 100 cm. the minimum temperature of about 14°C. is reached in January and the maximum of about 30°C., in July. We may assume that root activity is seriously hampered at temperatures below 20°C. so that the absorption of water by the Citrus trees is restricted in the period from November to March. This corresponds very well with the physiological behaviour of the trees in winter, when growth is checked and activity of all organs is diminished because of low temperatures of soil and air.

In May, a sudden rise of soil temperature to about 25°, which is probably optimal for the tree, is to be noted. A sudden drop occurs in November coinciding with the beginning of the rainy season. The maximum yearly fluctuation of the mean temperature at various depths, observed by us, was as follows: At a depth of 25 cm., 17.8°; at 50 cm., 16.6°; at 75 cm., 15.0° and at 100 cm., 13.4°.

We assume that these values are quite typical for a normal year at Rehovot. Our figures agree rather well with those of PERLBERGER (l. c.), who, however, found lower values in winter than those we had previously published for January in our first communication (53).

e) Wind Velocity. Wind velocity was measured by means of a cup anemometer manufactured by *Fuess*, Berlin-Steglitz. As said above the measured wind velocities range within relatively narrow limits. For the most part velocities from one to two meters per second were noted, and only in one case (19/III) the anemometer, which was always placed about 1.50 m. above the ground between two neighbouring trees, registered a value higher than five meters per second. This was due to a dry dusty SSW wind. Weak moisture-laden winds seem to be of minor importance in citrus transpiration. Accordingly we find it unnecessary to enter into further details as to direction (which was not always noted) and velocity of air movement, in connection with our investigations. Incidentally it may be mentioned that very heavy winds often do serious damage to the groves of this region. These appear as follows: west winds in the rainy period (damaging or destroying many fruits); hot east or south winds in spring from March to May, or in autumn from September to November; and cold dry east winds preceding the winter rains. The influence of these strong winds on citrus transpiration forms a special problem as yet little studied.

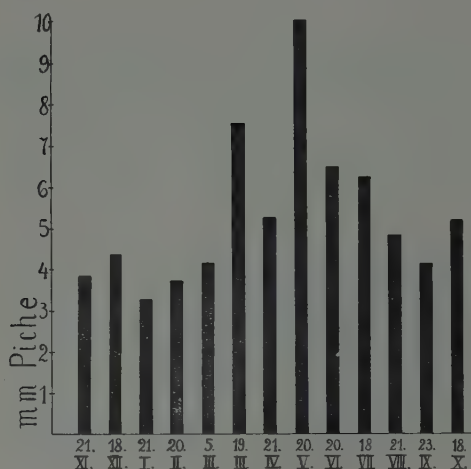
f) Evaporation: Measurements were taken with *Piche* evaporimeters made from ordinary burette tubes, according to directions by WALTER (77). Disks of ordinary green blotting paper, 3 cm. in diameter, were adjusted to the tubes and the apparatus was hung at a height of about 1.60 m. above the ground, on one of the main branches of the tree being tested. The relation between the amount of water evaporated and the surface of the blotting paper renders the factor used in changing water losses from cm³ into mm of open water surface. The factor is 0.91 for our instrument. These conditions correspond roughly to those prevailing in meteorological screens, the principal difference being that the rays of the sun penetrating through the peripheral leaves could sometimes directly touch the top of the instrument. Because of this, such measurements,

though deprived of much of their meteorological value, probably approach more closely the natural ecological conditions of leaf transpiration. Hourly evaporation values measured in this way ranged between 0 and 1.3 mm. per hour. Evaporation begins in the morning with values of about 0.09 mm. per hour, rises to its maximum of 0.45—1.3 mm. at about noon, and falls close to zero at sunset. A marked tendency towards earlier maxima was observed in our June, July and August measurements, i. e. in the typical summer months, when the daily maximum was attained between 10 and 11 o'clock. We are undecided as to whether this is associated with insolation or with special conditions of wind, such as the daily breeze from the Mediterranean Sea. Calculations of the departures from the hourly mean during the day time showed that positive departures are found between 9:00 and 15:00 in winter (October to March) and 7:00 and 16:00 in summer (April to August). Abnormal figures were found on the spring khamsin day of May 20th, when owing to extremely low humidity in the afternoon, all negative departures were observed in the morning, while afterwards departures remained positive till sunset. On September 23rd, positive departures were found from 9:00 to as late as 17:00 in the evening. This abnormal behaviour is easily explained by a strong wind blowing in the afternoon hours, in contrast to ordinary summer days, when the wind velocity decreases to zero at sunset. The highest positive departures observed were 0.50 mm. on July 18th (10:00 to 11:00); 0.53 mm. on March 19th (12:00 to 13:00) and 0.58 mm. on May 20th (12:00 to 13:00). Thus the days with the highest daily evaporation rates also showed the highest positive departures from the hourly average.

The influence of the Mediterranean Sea is reflected in the fact that differences between summer and winter losses are not as pronounced as would be expected from the high temperatures prevailing in summer. This corresponds to ASHBEL's (4) statements, made quite recently in this journal (p. 13) that evaporation at the coast is small in summer and great in winter as compared with other regions.

The sea does not exert so pronounced an influence in depressing evaporation on days when a dry east or south wind is blowing, as was the case on December 18th, March 19th and May 20th. In figure No. 2 a picture is given of the yearly march of evaporation as measured from dawn to sunset, with the daily sums of evaporation losses represented in the form of columns. A line connecting the tops of these columns forms a very regular "S" shaped curve, with the exception of the aforementioned three days, the columns of which jut out of it. October 18th also has higher values in spite of high air humidity, possibly because of cloudy weather combined with strong winds. WALTER (77) has shown that the wind increases evaporation more on cloudy than on clear days. It is seen that the evaporation values of the spring khamsin days, March 18th and May 20th, are about 60% higher than would be expected, considering the columns in the rest of the graph.

Under normal conditions, there is little or no evaporation at night, as the relative humidity of the air generally approaches 100%. Khamsin periods are exceptional in this respect also, and the hourly losses may reach considerable

**Fig. 2**

The daily evaporation from dawn to twilight in the course of the year as found on the days of measurement. Note the abnormally high evaporation on the khamsin days Dec. 18th, March 19th and May 20th.

figures. In the night of October 28th/29th, 1935, we measured evaporation losses amounting to 2.14 mm., between 18:00 and 6:00. The highest hourly value, between 21:00 and 22:00, was not less than 0.5 mm.* This is nearly as high as the maximum evaporation observed on ordinary autumn days during the daytime. If, therefore, evaporation in Palestine, on khamsin days, reaches often more than three times the normal amount [according to ASHBEL (4)], a considerable part of the surplus is probably to be accounted for by evaporation during the night.

Table No. IV represents the meteorological conditions of the above mentioned khamsin night.

TABLE IV.

*Humidity and evaporation during afternoon and night of the days
Oct. 28th and 29th, 1935.*

Hour	13	14	15	16	17	18	19	20	21	22	0	2	4	6
Humidity (%)	20	27	38	42	47	52	52	30	25	41	62	66	77	82
Evaporation per hour (cm. ³)	0.40	0.60	0.65	0.30	0.20	0.15	0.25	0.30	0.45	0.55	0.10	0.15	0.05	0.10
Temperature (°C)	33.3	31.0	28.8	27.4	25.1	24.0	23.8	24.3	23.8	20.8	20.5	19.6	20.1	18.7
Wind direction & force	—	—	—	—	—	0	?	ESE	ESE	SE	0	ESE	0	SSE
							1	1	2—3	1—2		1		1

*) During khamsin nights of October 1937, losses four to five times larger have been recorded.

The table shows that evaporation, having reached its peak at 15:00, sinks quickly to a low figure at 18:00, with decreasing temperature and rising humidity of the air. After sunset, a dry wind, which has not yet set in at 18:00, arises. Consequently evaporation rises again to a surprising degree, reaching at 22:00 a figure nearly as high as the maximum value of the afternoon. At midnight, the wind again abates and with humidity increasing greatly, evaporation sinks down to a very low level which is maintained till sunrise.

The behaviour of the *Piche* evaporimeter during this day and night confirms the observation of many authors that evaporimeters are strongly influenced by wind and much less sensitive to radiation (whereas the leaves of plants are much less affected by winds than by the rays of the sun). [See MAXIMOW (48); SEYBOLD (66)].

II. Internal factors (including physiological indicators of water balance):

It is well known that the transpiration process is regulated by the plant. The chief regulators are the stomata of the leaves. Whenever conditions of water supply become adverse, they react by closing. As there is as yet no convenient method of studying the condition of the apertures of stomata on citrus by direct observation, indirect methods have to be adopted. We used the infiltration method, which though by no means ideal, is easy to apply. Further information about the diffusive capacity of the stomatal pores was obtained by STAHL's (69) cobalt-chloride method, which was used by us (as reported in a former publication) as an approximate indicator of the intensity of transpiration. In this way we hoped to check the adaptability of this method to measurements of citrus transpiration.

The sap concentration of the leaves is considered by WALTER (78) as an indicator of the water balance. This author found that its values as determined by the cryoscopic method, rise (1) when the water reserves during the hot hours of the day are not replenished by the transpiration stream rising from the roots; and (2) when, at certain seasons, the water suction of the roots is checked either by the low temperature or by the dryness of the soil. The investigations of HAAS and HALMA (28) have shown that this method is applicable with success in studies of the seasonal water balance of lemon and orange trees.

Another method of studying the water requirement of the leaves at a given moment, which is inversely proportional to the adequacy of the water supply, is comparison of the weight of branchlets or single leaves, when just plucked from the trees, with their weight after artificial saturation with water. The difference between the values is called "Water Saturation Deficit". While American authors [HALMA, 1934 (31), COMPRON, 1936 (20)] call the difference in percentage of fresh weight of the leaves, "relative saturation deficit", we prefer to follow STOCKER's suggestions (73) to calculate this difference in percentage of the maximum water content (STOCKER's "Wasserdefizit"). We believe his method is preferable as it gives a direct measure of the decrease in the water reserves undergone by the leaves, eliminating dry weight, which varies greatly during their lifetime. Though STOCKER's (73) method involves

the additional work of the determination of the dry weight, we propose its general adoption in citrus research in order to facilitate the comparison of values established in various countries.

The following particulars illustrate the manner of execution of these measurements and their results:

1. *Stomatal aperture.* As reported in our former publication, we made use of the following sequence of DIETRICH's scale of liquids, chosen by PISEK and CARTELLIERI (1931) (59, I), for our infiltration experiments; (1) xylene, (2) petroleum, (3) a 1:2 mixture of castor and turpentine oils and (4) liquid paraffine. The speed of penetration was designed by the designations I, II, III and Δ , which denote various degrees of velocity of the appearance of the infiltration spots. The various degrees (1—3) used by P. and C. to indicate size and number of the spots were also noted, but were left out of consideration in the final calculation, as it was found that the spots fuse quickly, so that it is difficult to get an idea of the number of infiltrated pores in this way.

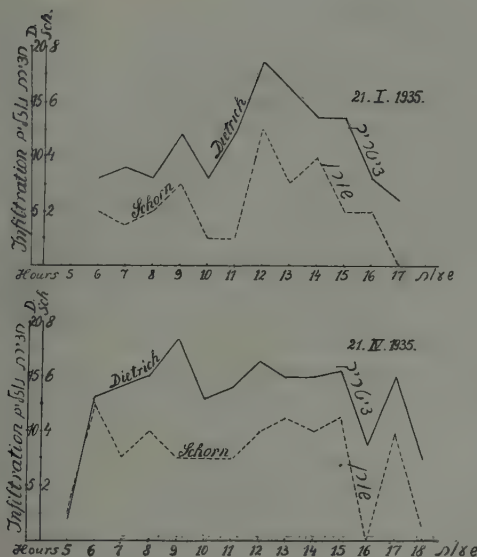
In addition to these liquids, we have made use, since December, 1935, of mixtures of isobutyl alcohol and ethylene glycol, as indicated by SCHORN (65). These liquids are mixed in proportions differing from one another by ten-volume per cent. Whereas the pure alcohol (liquid No. 1) is supposed to penetrate slits slightly open, pure glycol does not penetrate even very wide apertures. We found that these liquids are quite suitable for work with citrus leaves. In the early morning, or late in the evening, only liquids Nos. 1 or 2 (90% alcohol + 10% glycol) penetrate, while in the sunny hours, liquids Nos. 3, 4 or rarely 5 and even 6 may infiltrate. The number of the last liquid to penetrate is used as a measure of stomatal aperture.

In accordance with SCHORN's (65) experience, we found, in most cases, a close correspondence between the infiltration results of both systems.

Fig. No. 3 represents the march of stomatal aperture, as found in our April and January measurements (represented separately in DIETRICH and SCHORN scales). It is noted that the general march of the curves agrees quite well with one another, especially if the general level of opening is sufficiently high, as it was in April. Drops to zero of the SCHORN values are found in both curves represented.

We decided to combine both in our calculations by adding to the sum of the values of the speed of penetration of the four DIETRICH liquids, the number of the last liquid of SCHORN's scale to penetrate. Thus we hoped, to obtain more reliable results. In this manner the additive values of our diagrams have been established as sums calculated from two leaves examined every hour*). A given value, 10, in the morning might indicate, for instance, that of DIETRICH's liquids,

*) If infiltration with a tested liquid took place only at solitary spots, ["g. v." at PISEK & CARTELLIERI (59, I)] we calculated its value as $\frac{1}{2}$ in the final addition.

**Fig. 3**

The apertures of the stomata in light as measured by Dietrich's and Schorn's liquids on Jan. 21st, 1935 and April 21, 1935. Note that the scales for the two liquids differ.

only petroleum and xylene penetrated (in 2 leaves which were investigated) with the velocity degree II, while only liquid No. I of SCHORN's scale penetrated: $2 \times [\text{II (petroleum)} + \text{II (xylene)} + \text{I (SCHORN)}] = 10$.

Leaves in the sun, as well as in the shade, were examined, but we have refrained from publishing the shade measurements in all cases where only one leaf had been tested per hour. Thus, all published curves of daily stomatal aperture represent the average of at least two, and at most, three leaves tested per hour. If old as well as young leaves were found, we tested one old and one young leaf, both in light and shade, and calculated the averages in light and shade, irrespective of the age of the leaf. Thus, we found values, which in many cases, seemed to explain the march of the transpiration process in a satisfactory manner.

The SCHORN liquids have the disadvantage that even liquid No. I does not penetrate into orange leaves when the slits are very narrow. Thus infiltration values drop to zero when there are still clearly visible infiltrations with petroleum and xylene. The DIETRICH liquids, on the other hand, have the disadvantage that petroleum and xylene behave in nearly the same way when applied to the orange, and that in general, there are cases when one liquid, supposed to infiltrate less than another, does infiltrate, while the other infiltrates to a weaker degree or not at all. It is easily understood that liquids of such varying natures as these DIETRICH fluids, are influenced differently by temperature as regards their surface tension, viscosity, etc., and that their application in the cool morning hours will have affects unlike those found at noon.

Some general rules can be derived from our numerous observations, which are not published here in detail.

1. Wide open stomata are infiltrated to a high degree, instantaneously by petroleum and xylene. Turpentine-Castor oil mixture and liquid paraffin penetrate more or less easily. Liquids 3 or 4 generally mark the limit of penetration of SCHORN's scale.

2. Moderately open stomata as found in the early morning and late afternoon hours or during stomatal restriction of gaseous exchange in the hot hours of the day are in general not penetrated by (a) the turpentine-castor oil mixture; (b) liquid paraffin and (c) SCHORN's liquid No. 3. We wish to cite as an example the restriction of water loss recorded on June 20th between 12:00 and 14:00, which coincided with the failure of these three liquids to penetrate, whereas they did infiltrate at 11:00 and 15:00.

3. Closed stomata, tested at night or at dawn, are impenetrable to any of the liquids. At most a few single infiltration spots are caused by petroleum or xylene.

So far, we are unable to say what widths of aperture (in microns) correspond to these infiltration degrees. On the occasion of a visit to Prof. STALFELT's laboratory at Stockholm, the senior author convinced himself that there is a possibility of making direct measurements by means of STALFELT's method of observation (72). This may possibly enable us to coordinate the size of the apertures with infiltration values in the future.*)

2. Cobalt chloride paper as an indicator of stomatal transpiration. As described in our first publication, we made use of standardized paper, ($KP\frac{1}{2}$), prepared according to the directions of LEICK (46). The leaf was enclosed in a frame used for making photographic copies, so that a strip of the paper crossed the leaf obliquely. The lower surface of the leaf was exposed to the light for five minutes and then the percentage of the strip coloured red was estimated. Beginning with February 1935 we changed the system slightly. The whole surface of the leaf was covered by a disk of ($KP\frac{1}{2}$) paper. In this way the great differences between transpiration rates in various areas of the same leaf could be eliminated in the estimations. When summer conditions began we had to shorten the period of exposure from five to two minutes, as the paper changed colour very quickly. Even this modification of method proved insufficient under conditions of very strong transpiration. (Cobalt chloride paper $KP\frac{3}{4}$ or KPI (LEICK) would probably have given better results). Beginning with February, we exposed three leaves every hour: two sun leaves and one shade leaf. The frames containing the former were placed in the sun and those of the latter in the shade. The sun frames were exposed at a right angle to the sun.

*) Mrs. MINA NADEL recently established in our laboratory that with various plants other than *Citrus* high infiltration degrees correspond to medium apertures while medium infiltration degrees were characteristic of very small apertures. Direct observations of citrus stomata *in situ* met with great difficulties.

The curves showing the coloration of the cobalt chloride papers are given in our synoptic diagrams. They represent the averages of two sun leaves. Shade values are not represented as only one leaf had been measured per hour. Just as in the transpiration weighings, we often found very great differences between the two sun leaves, which we chose at random. Thus on March 5th, at 11:00, 85% of one leaf and 15% of the other turned red. These are exceptionally great differences, but variations amounting to 50 or 60% of the higher value were quite usual. We assume that these differences correspond, at least in part, to the behaviour of the leaves on the tree, as they are quite analogous to differences in water loss, determined with the transpiration balance, and to measurements with the infiltration liquids. Observations with all these methods lead to one and the same conclusion, namely, that the stomata behave in a very individual manner in different leaves and on different areas of the same leaf.

The daily course of the cobalt-chloride values corresponds quite well, in many instances, with the transpiration curves, as for example, in the measurements of March 19th, September 21st, November 21st and December 18th. In other cases there is less agreement. A better correspondence is not to be expected as there are the following sources of error in the cobalt-chloride method: Conditions of transpiration are quite different within the frame and outside it as regards temperature, saturation deficit and air movement. In addition, under certain conditions, at least, changes in stomatal aperture may possibly take place during the exposure in the frame. It cannot be expected that the average values of two leaves, chosen at random for the cobalt chloride test, should agree closely with the average of two other leaves, chosen for weighing. Last but not least, it seems that the changes in colour, observed by us, cover only the medium range of the process of water absorption by the paper. Small amounts of water vapour absorbed may be insufficient to produce a clearly perceptible change in colour, whereas, on the other hand, 100% colouration was often reached, so that it was impossible to differentiate between degrees of very strong transpiration. The conclusion that the number of units of paper area changing from blue to red is possibly not proportional to the quantity of water vapour leaving the leaf, can also be drawn from the fact that in some instances a small drop in transpiration established by the balance, corresponded to a far greater drop in the cobalt-chloride value (as in the November and December measurements). This can be explained in two ways: Either a certain amount of vapour escaping at first is insufficient to produce any change of colour as discussed above, or we may imagine that the process leading to the establishment of an equilibrium of vapour pressures within the closed chamber of the frame sets in quickly if the stomata are wide open, but rather slowly if the slits are narrow. In the latter case, exposure for two minutes may be too short a period to produce a gaseous exchange adequate to the concomitant loss at the balance, where the exchange is favoured moreover by air movements. At any rate, these considerations demonstrate that the comparison of transpiration losses in the free atmosphere with those in closed chambers, presents quite a difficult problem in itself, which is further complicated by the comparison of losses in grams, in one case, with changes of colour, in the other.

3. Concentration of cell sap. In determining the cell sap concentration (osmotic value) of leaves, we made use of the methods described by WALTER (79) i. e. the leaves were killed by heat, the sap expressed with a laboratory press and the cryoscopic determination of the freezing point made by means of the micro-method of DRUCKER-BURIAN. This method has recently (1936) been adopted by HALMA (33), so that the comparison of such measurements carried out in Palestine with those made in California is facilitated.

For each determination, 15—25 leaves were chosen at random in the hope of getting a typical picture of the changes occurring during the day as well as in the course of the year. Table V gives the results of these determinations, made every three hours, on all days when measurements were taken.

TABLE V.
Osmotic value of Jaffa orange leaves (in atmospheres).

Date	6:00	9:00	12:00	15:00	18:00	Daily average	Largest daily fluctuation
October 18th, 1934	16.24	19.12	19.48	19.00	17.56	18.28	3.24
November 21st	17.38	18.11	18.88	18.26	18.10	18.15	1.50
December 18th	20.08	20.44	20.24	21.22	20.26*)	20.85	2.14
December 20th	—	20.38	21.11	20.26	—	20.35	?
January 21st, 1935	20.50	21.28	21.46	20.98	20.50*)	20.94	0.96
February 20th	22.60	23.20	23.68	23.20	—	23.17	1.08
March 5th	22.84	23.08	23.62	22.12	21.10*†)	22.55	0.78
March 19th	18.70	21.52	24.99	23.20	21.70	22.02	6.29
April 21st	23.44	21.10	19.72	21.46	22.18	21.58	3.72
May 20th	21.28	22.18	21.28	21.22	20.26	21.24	1.92
June 20th	19.66	18.64	23.80	19.24	19.26	20.24	4.14
July 18th	18.94	19.36	18.40	19.90	21.58	19.64	3.18
August 21st	21.98	19.76	21.14	21.50	19.76	20.83	2.22
September 23rd	20.20	19.21†)	20.56†)	21.45†)	22.12	20.71	2.25

*) Values taken at 17:00 instead of 18:00.

†) Average of two determinations.

The following general conclusions seem justified on the basis of these determinations:

(1) The general level of the osmotic values corresponds quite well with that established for Washington Navel orange leaves by HAAS and HALMA (28) $\Delta = 1.431 - 2.213^{\circ}\text{C}$ i. e. 17.00—26.59 atm., and by HALMA (33) who found 20.74 — 26.19 atm.

(2) The daily march of our values seems to justify the use of these figures as a physiological index for the water balance of the trees only in winter.

In the measurements of October 18th, November 21st, December 18th, January 21st, March 19th and May 20th, the trend of the values is apparently produced by changes in the water expenditure in the course of the day. This, however, cannot be the case in the April, June, July, August and September measurements, when other factors evidently interfere. The figures of these measurements showed irregular fluctuations and even an inverse relationship to the increasing water expenditure during the day.

There can be no doubt that our summer values are not as representative of the whole tree as the winter values seem to be. HAAS and HALMA (28), studying the osmotic values of citrus leaves, found that they were greatly influenced by two factors; (a) insolation and (b) new growth. For this reason these authors, in their later study of the yearly march of these concentrations, were obliged to choose branches from the shady side of the tree, at a certain hour of the day, and to take into consideration the fact that the osmotic value of existing leaves decreases at the time when new shoots are formed. Probably the fact that we chose our leaves at random from various branches, during the summer (when new shoots are formed and certain branches are probably losing much more water by direct insolation than others), gave rise to the abnormal march of our values. We assumed that one sample of leaves (taken in the manner described above) would render values of osmotic pressure representative of the whole tree. This assumption, however, seems to be incorrect at least under summer conditions. While two samples plucked in the above manner rendered exactly the identical value on March 5th at 17:00 (21.10 atm.), we found very great differences between other such double samples, which were taken on Sept. 23rd. At 9:00 two samples rendered the values 21.10 and 17.32 atm. respectively. At 12:00 the values were 21.40 and 19.72 and at 15:00, 23.14 and 19.78 atm. respectively. For this reason, our summer values can be considered merely as examples of single determinations and not as averages characteristic of the behaviour of the tree on the days of measurement.

(3) The yearly march of the average daily values shows, in correlation to the determinations of HAAS and HALMA (28), a definite trend towards higher values in winter, when soil and air temperatures are low. This rise sets in in November when, as we have seen, soil temperatures drop considerably. On December 18th, there was a pronounced rise in comparison with October and November values. At the same time, soil temperatures dropped to about 16°C. a figure corresponding exactly to the figure of 60°F., considered by HAAS and HALMA (28) as characteristic for the beginning of the seasonal rise in osmotic values. Fig. No. 4 shows roughly an inverse relationship between soil temperature and osmotic pressure during the winter months.

The highest value was reached in February. Beginning in March a slow and inconstant decrease of the values occurred, lasting until November, when the minimum figure of the year was attained.

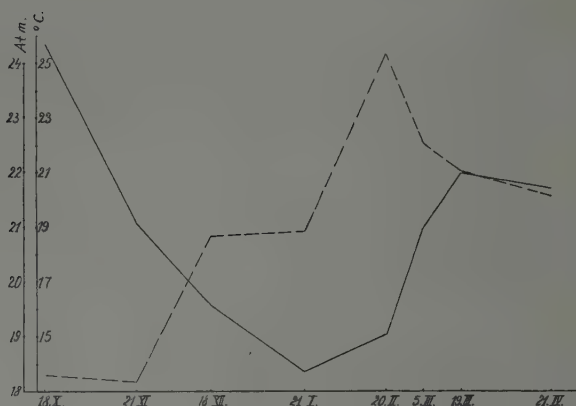


Fig. 4

Soil temperature and osmotic value of the leaf sap during the winter months.

— soil temperature (°C), ---- osmotic value (Atm.)

(4) In winter (November to the beginning of March), when transpiration rates are low, we find small daily fluctuations of the osmotic value, whereas these are rather large in the warm period.

4. Water Saturation Deficit. The Water Saturation Deficit (W.S.D.) was determined according to the directions given by STOCKER (73), with the exception that we did not cut the petioles a second time, as the stumps produced in this way are easily lost, so that many leaves would have to be discarded. After saturation the leaves were dried in an oven at 75°C., and their dry weight determined.

By subtracting the dry weight from both the natural and the maximum fresh weights, the natural and the maximum water contents, respectively, are found. The water saturation deficit is then calculated according to STOCKER's formula:

$$\text{W.S.D.} = \frac{\text{Maximum water content} - \text{natural water content}}{\text{maximum water content}} \times 100$$

Leaves which gained less than 1% in weight by suction or even lost in weight through respiration, were discarded. Only when a gain as small as 1% occurred in the early morning or in the late evening, when saturation deficits are generally small, did we use such values in the calculation of the average.

In order to give an approximate idea of the relation between our values and those of HALMA's (31) Relative Saturation Deficit, the following formula may be of some use:

W.S.D. (STOCKER) = $\frac{3}{2}$ R.S.D. (HALMA) (with *Citrus* leaves). This formula is based upon our experience that water comprises about $\frac{2}{3}$ of the fresh weight of the leaves.

For the most part, the values of the W.S.D. found during this investigation range between 1 and 7% of the maximum water content. Even on khamsin days no higher figures were found owing to the favourable water conditions of the soil, on the one hand, and the regulative capacity of the tree, on the other. After an extended khamsin period in November, 1933, values as high as 14% were found, under dry soil conditions. Since then such figures have not been reestablished.

Our values which are represented in the daily transpiration diagrams, agree quite well with those of HALMA, for Washington Navel oranges. Under favourable water conditions of the soil, at noon, the values of this author approximate 4% R.S.D. (HALMA), or 6% W. S. D. (STOCKER). This is a figure similar to the daily maximum values established by us in the same months of the year (June to October).

It is remarkable that the saturation deficit shows a close and constant relationship to the daily march of transpiration, in all our measurements. In the morning (6:00), values were generally quite low, rarely exceeding 2% (July, August and December). In summer, when morning transpiration caused a great loss of water, maximum values (4—7%) were found at 12:00 or 15:00, and sometimes even as early as 9:00 (August and September). In the evening, values again dropped close to 2%. At times, the general trend of the saturation deficit curve runs more or less parallel to that of the transpiration curve, as on June 20th, July 18th and August 21st, i. e., especially in the summer months, when the daily fluctuations are relatively large.

Thus, we get the impression that the water saturation deficit gives quite a reliable physiological index for the water balance of orange and other trees in accordance with our previous observations [OPPENHEIMER, 1932 (52) and OPPENHEIMER and MENDEL, 1934 (53)].

D. ORANGE LEAF TRANSPIRATION.

I. *The method used in studying transpiration.*

The fact that there exists no physiological theory of the use of irrigation water is easily accounted for by the extraordinary difficulties of finding a satisfactory method for the determination of the water use of trees naturally rooted in the soil. The progress made in the elaboration of field methods for the study of transpiration by German authors [PFAFF (56), STOCKER (74), HUBER (37)] seems, however, to have paved the way sufficiently so as to stimulate research in this field. In their studies of plant transpiration the said authors carried out rapid weighings of freshly plucked leaves. According to the suggestion of HUBER (37), a "transpiration balance" was manufactured by *Hartmann and Braun*, Frankfurt o. M. We used this

instrument, which allows accurate weighings of milligrams and the estimation of half milligrams.

Historically, the method of rapid weighing for the establishment of natural transpiration losses was first used by PFAFF (56) in his researches on the transpiration of an oak tree, published in 1870. The problem upon which this author was working was the same as that which forms the ultimate object of our researches, namely, to determine the quantity of water escaping to the atmosphere from a leaf-bearing tree in the course of an entire seasons's growth. PFAFF (56) tested the tops of branchlets, which he plucked from the tree, weighed immediately, and then reweighed after having exposed them for three minutes in a shady place in the open, close to the tree. He assumed that the loss in weight established in this way represented a minimum value closely approaching the natural loss of the branchlet. He was well aware of the fact that the transpiration of the severed branchlet showed a tendency to decrease. The loss of the first two minutes was found to be higher than that of the subsequent two minutes. He, however, did not observe the rising values after the severing of the branch, which were remarked by several modern authors [IWANOFF (41), KAMP (42)]. When BURGERSTEIN published his monograph (17) on plant transpiration in 1904, he considered the weighings of cut parts of plants to be a source of information which could give a satisfactory answer "nur auf gewisse Transpirationsfragen" (p. 6), and added that experiments of this kind ought not to be prolonged for more than one or several hours (!). This remark shows that the valuable method of short period weighings had not been made use of again since its invention by PFAFF.

It has recently been reintroduced to the practices of modern experimental ecology by B. HUBER (39). He first made use of it in his excellent research on the fluctuations of transpiration intensity depending upon the height of insertion of the branches on the stem. Later workers also employed this method. STOCKER (75,1) calls the practice of his short period weighings in the form used, "ein neues Verfahren zur Bestimmung der momentanen Transpirationsgrösse", (1931, p. 497), while ARLAND (1929; 2), the author of the "Anwelkverfahren", admits that, "auch schon in früheren Jahren verschiedene Autoren mit abgeschnittenen Pflanzen und Pflanzenteilen gearbeitet und versucht haben . . . , teils ohne Wasserzufuhr die Stärke

der Transpiration an diesen festzustellen". In recent years the method has found an ever increasing application by various European workers and is now considered quite reliable by most competent experts, including HUBER, STOCKER and also MAXIMOW (48). Critical contributions as to its reliability were published by IWANOFF (41), PFLEIDERER (52), SCHRATZ (63) and FUKUDA (25).

Whereas IWANOFF (41), working under the climatic conditions of Leningrad, found an increase in transpiration rate after severing branches from forest trees, SCHRATZ (63) using the same method, showed that in plants studied by him in Arizona, the values were often found to be too low. This author established the fact that in most cases, after severing a leaf, transpiration decreases rather rapidly, reaching a more or less constant value in the course of the first hour, often even after 10 to 15 minutes. He, as well as WASSILIEW (80), found, in some cases, a slackening of the transpiration rate as early as in the second minute after picking. SCHRATZ (63) justly points out that transpiration values resulting from the immediate weighing of plucked leaves can be considered as typical of leaves still connected with the plant only in the case that subsequent weighings fail to show decreasing rates. This is true of many succulent plants.

PFLEIDERER (57) investigated the question of whether the transpiration from the top of small potted plants that had been separated from the root system remained for some time more or less equal to the values established before the plant had been cut. Working with a considerable number of species, this author arrived at the conclusion that the transpiration rate remained practically unaltered. He found changes in the transpiration rate after cutting amounting to $\pm 20\%$, but the average of all his experiments closely approached 100% of the figures established under normal conditions.

As shown by SCHRATZ (63), speed is an essential condition if values approaching the true transpiration rate of the uninjured leaf are to be found by this method. We worked rapidly enough so as to finish the first weighing from 30 to 55 seconds after the severing of the leaf. The second weighing was made about two minutes later.

In measurements carried out in September 23rd, 1935, we compared the water loss of leaves during the first minute after the first weighing with that during the second minute. The latter, expres-

sed as a percentage of the former, was found to range, in 17 cases out of 23, within the limits of 80 to 120%. Eight morning weighings yielded an average value of 98%. In 12 afternoon weighings (13:00—15:00) the agreement was less close. The average loss of the second minute was 122.4% and in three cases, single values rose as high as 144.8, 177.7 and 195.5%. In the evening (16:00 to 17:00) three weighings again yielded more consistent results. The average relative loss of the second minute was 95.1% of the first. The highest figure amounted to 122.6%.

We feel justified in interpreting these numbers in the following manner: 1) Although deviations are large and the single values fluctuate considerably, there is no tendency towards a decrease in transpiration intensity within the short period chosen by us for the weighings. On the contrary, a marked tendency towards higher values could be established in that afternoon. Such behaviour seems to agree with the theory of IWANOFF (41), who assumes that the relaxation of the water columns in the vessels at the moment of plucking causes a rise in the vapour pressure in the intercellular spaces of the leaf and thus favours transpiration. On the other hand the increase in transpiration intensity might be explained by stomatal movements during the first three minutes after the severing of the leaf.*) This however, seems unlikely as we were unable to establish such changes in stomatal aperture neither with the infiltration method nor by porometric readings. The infiltration tests showed that stomatal regulations set in only about five minutes or more after the plucking of the leaf, leading to a very marked reduction in the intensity of transpiration. In order to check the results of these observations, the effect of the severing of the leaf on stomatal behaviour was also tested by porometric measurements. Using PINKHOF's (58) porometer, the following results were received: Porometer times showed no appreciable change during the first ten minutes after the leaf had been detached. Sometimes a small increase was observed but more frequently we found, immediately after the separation of the leaf from the branch, a small reduction in the time needed for the fall of the water column through a distance of one centimeter. After ten

*) General considerations suggest that leaves with a pronounced xeromorphic structure such as mature orange leaves should be little influenced in the cuticular portion of their transpiration by the separation from the tree.

minutes, porometer times were found to increase markedly, indicating a reduction in stomatal aperture. One series of observations will illustrate the course of the measurements. In a mature leaf tested on July 20th, 1936, under an unclouded sky, we established from 15:52 to 16:05 an average porometer time of 29 seconds. From 16:07 to 16:16 the average time of ten observations was 26 seconds. The leaf was then detached. In the next five minutes the porometer times were: 25, 25, 26.5, 27.5, 27.5 and 29.5, seconds, i. e. the fluctuations remained within the same limits as before, starting at a slightly lower level and passing slowly to higher values. At 16:26 the porometer time jumped quite suddenly to the value of 34 seconds, remaining as high as that or a little lower till 16:31. At 16:38 a new reduction of the stomatal openings lead to a further increase, namely 60 seconds. Later the porometer times became increasingly longer, rising at 16:52 to 137 seconds.

From these porometric observations it would appear that no immediate stomatal movements occur when an orange leaf is torn from the branch during the day, and that weighings within the first three minutes would render values similar to the transpiration loss before the leaf had been plucked. We suppose that an increase in transpiration rates observed in the second minute is to be explained by IWANOFF'S (41) theory or by changes in external conditions, whereas decreasing rates can be explained by the latter possibility alone, if stomatal movements have been excluded.

The question, as to what extent the water loss of single plucked leaves would be uniform enough as to approach closely the average loss of all leaves of the tree, was studied, at our suggestion by MISS T. ELAZARI-VOLCANI, with potted plants of the Sweet Lime (*Citrus aurantiifolia* Sw. var. *dulcis*). It was found that neighbouring leaves of similar structure differed to a surprising degree as to their transpiration intensity, even under the same external conditions. In some cases, the average water losses of three or six leaves corresponded to the average loss of the whole plant. In others, there was no such agreement. This is by no means surprising as a relatively small number of leaves was weighed, the average loss of which might differ from the average loss of the entire tree because of differences of insertion, illumination and age. In fact, various authors (BARTHOLOMEW, HUBER (1923) have noted the fact that there may be

great differences in the transpiration losses of leaves inserted in the same sections of the same branch. As BARTHOLOMEW (6) (p. 769) explains, "a given citrus leaf may be more efficient or it may be less efficient in resisting the loss of water than the adjacent or nearby leaf on the same branch". BARTHOLOMEW found this irregularity to be more pronounced in orange than in lemon trees. We have found this author's statements to be true of the Jaffa orange. While in the majority of cases, two or three similar leaves showed similar behaviour as regards their water losses, there were other cases with strongly diverging values. This is illustrated by the following table showing the single values of the measurements taken on July, 18th, 1935:

TABLE VI.

Transpiration intensity of single Jaffa orange leaves, weighed on July 18th, 1935 (milligrams per gram of fresh weight per hour).

Hour	In the light			In the shade		
	Leaf weighed first	Leaf weighed second	Difference in % of lower value	Leaf weighed first	Leaf weighed second	Difference in % of lower value
4:00	0	16*	—	—	—	—
5:00	21*	14*	50	0	—	—
6:00	354	394	11	180	115	56
7:00	503	499	1	189	165	15
8:00	752	504	49	358	305	17
9:00	747	958	28	510	569	11
10:00	491	671	37	653	649	1
11:00	787	847	8	581	509	55
12:00	552	851	54	900	723	24
13:00	660	1705	158	754	846	12
14:00	632	926	46	464	450	3
15:00	600	689	15	402	529	32
16:00	731	743	2	272	137	98
17:00	733	543	35	126	125	1
18:00	152	71	114	34*	26*	31
19:00	23*	0	—	0	—	—
Total	7638	9431	Aver. 29.1	5423	5546	Aver. 27.4

*) Values not reliable, absolute transpiration losses being as low as 0.5 to one milligram.

A glance at the table shows a remarkable agreement in some cases and deviations approaching 100% in others. In one case, under extreme conditions, the deviation reached as much as 158%. While under these circumstances it is not certain that the hourly losses as based upon three to four weighings per hour are typical for the entire tree, we believe that this is the case for the total daily loss of the average leaf, and this is of much greater interest from an agricultural point of view. The daily sums of the losses in the shade agree to 2.3%, while in the sun there is 23.7% deviation, probably an unusually high figure, produced by the strong differences at 13:00. The daily sums of the losses of the first and second leaves weighed in the sun on Nov. 21st, were 4465 and 4485 milligrams respectively. In this connection it seems important to add that our measurements of 1934/35 were checked in part by similar weighings, carried out in 1937 on the same trees, when six to eight leaves were weighed per hour. The results approximated those published here and a quite similar march of the hourly losses was established for the summer months.

Since then MISS ELAZARI-VOLCANI (21) tackled the complicated problem of the behaviour of single leaves as compared with that of entire plants as far as transpiration is concerned, from another angle. The transpiration losses of single sour orange leaves plucked from six year old trees in the grove were compared with the losses of two year old, well watered trees of the same species, which were rooted in pots and exposed to identical outdoor conditions of typical Palestinian hot and sunny summer days. A striking similarity of the shape of the curve in the diagrams representing the daily march of transpiration was established. This seems to indicate that with due caution, the transpiration of a few leaves of citrus trees may be considered as roughly typical of the behaviour of the whole plant. Indeed, this assumption is made by all plant ecologists who employ the method of short period weighings in the investigation of the behaviour of plants in the open. ARLAND (1), however, established that in the cases which he investigated, such an assumption was unjustified.

It has further been shown by HUBER (39) that the height of insertion on the tree plays an important part in determining the transpiration intensity. This was demonstrated by him in *Sequoia*

gigantea, where transpiration intensity in branches two meters above the ground was found to be about twice as great as in branches inserted at a height of 14 meters. This would mean that in calculating the loss of the whole tree from single leaf weighings, a note must be made in each case of the height from which the weighed leaves were chosen. The trees chosen by us were only about 2.50 meters high and, as HUBER later pointed out, the differences in transpiration intensity depending upon height are by far lower in more xerophilous trees (*Quercus* and *Pinus*) than in *Sequoia gigantea*. We suppose that the height of insertion plays a minor part in young citrus trees, though we admit that the subject requires further attention. In our experiments the leaves weighed were inserted, in most cases, between one and two meters above the ground.

Another difficulty arises in the interpretation of transpiration losses for the whole leafy crown of a tree in the consideration that leaves may interfere with one another's transpiration considerably, as was demonstrated by FILZER (23). This worker established the interesting fact that plants forming dense lawns on wet soil lose much less water when growing in associations than when isolated.

On the other hand, plants in associations which were less dense, growing on a rather dry soil, with xerophytic leaves, arranged more or less vertically, in a windy situation, showed transpiration losses rather closely approaching those found outside the association. It could therefore be expected that in the leafy crown of an orange tree the influence of the leaves upon one another as regards transpiration intensity would be of no great importance in general, particularly not during the summer irrigation period.

Experiments carried out with a *de Nice* orange tree on June 24th and 25th, 1936, support the view that these interesting relations between individuals of the same association, which would seem theoretically to be applicable to the leaves of trees and shrubs, do not play an important part as far as orange trees are concerned. 17 transpiration weighings were made at noon, in the afternoon and again on the following morning, exposing the plucked leaves for about one minute at their point of insertion and for another minute outside the top. In ten cases the leaf was hung first within the foliage and then outside. In eight cases the order was reversed. The results were quite inconsistent. When the leaves were hung first within the foliage

losses were greater outside the tree in four, inside also in four and practically equal in two instances. When they were exposed at first outside, the corresponding relations were: greater losses outside 4, inside 3, equal 1. From these observations a depressing influence of neighbouring leaves on the transpiration cannot be established. The integrated relative losses of all the experiments showed even a decidedly higher figure for the leaves placed at their natural point of insertion. At the beginning of these weighings a strong west wind was blowing, whereas at the time of the morning experiments, the winds were very mild. Even under these conditions, no higher losses could be established outside the tree. It may be that under wet winter conditions, this "Filzer effect" may be of some importance for low shaped trees. In the present investigation, however, we have neglected this possible source of error.

All in all, 14 series of measurements were taken, beginning October, 1934, and ending September, 1935, mostly about the beginning of the astronomical month (e. g. Sept. 23rd, 1935). Every hour from three to four leaves were weighed, two from brightly illuminated branches and one to two from shaded ones. In cases where young leaves had been formed, both young and mature leaves were weighed. The great number of meteorological and physiological measurements taken every hour rendered the execution of more weighings per hour impossible.

In spite of all the theoretical difficulties, the results of our weighings correspond remarkably with well established facts in the ecology of plant and especially Citrus transpiration. Consequently we feel justified in publishing them here, with all due caution as regards the question of whether our values can be considered as the real natural losses of the leaves or only as approximate figures.

II. *Daily march in the course of the year.*

1) *Transpiration in the sun.*

Fig. 5 represents the march of transpiration of leaves exposed to the sun, on October 18th, November 21st and December 20th. It is seen that the intensity of transpiration, on October 18th, rose abruptly from 5:00 to 9:00 reaching the remarkable figure of 1177 mg. per gram of fresh weight per hour. One of the three leaves weighed at 9:00, transpired as much as 1792 mg/g.h! At 10:00, transpiration

dropped considerably. A second summit was reached at 12:00 (855 mg/g.h). At 13:00 a second drop set in, followed by a third peak at 14:00 and 15:00. A striking feature of days with extraordinarily high values of water loss in the morning hours is the lower level of transpiration in the afternoon. Corresponding to this general experience, a sudden drop set in as early as 15:00, leading to a practical standstill of the transpiration process at sunset (17:00), when only 32 mg/g.h were lost by transpiration.

mg/g.h

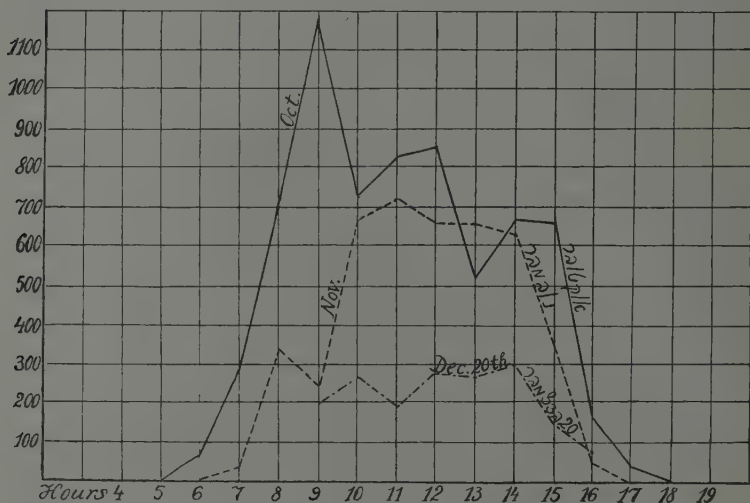


Fig. 5.

The daily march of transpiration in sun light on Oct. 18th, Nov. 21st and Dec. 20th.

On November 21st, transpiration set in one hour later, and reached a much lower maximum value (712 mg/g.h) than in October. The course of the transpiration rates, in the sun, between 10:00 and 14:00 was quite steady. At 14:00, the usual evening drop observed in all curves, began. Transpiration dropped to very low values at 16:00 and stopped completely at sunset (17:00), at which hour two leaves, weighing nearly 1000 mg each, were found to lose 0 and 1 mg. respectively, in the course of five minutes.

In December, two series of measurements were taken, one complete, from dawn to twilight, on December 18th, a bright, almost cloudless day, with uncovered sun throughout; and a second incomplete, not starting before 9:00, on December 20th, a rainless, but cloudy day. Both days are typical of this season. The former is not represented in figure 5, as the transpiration curve resembled, in every respect that of November 21st, the total daily loss even surpassing that measured in November. The transpiration curve of December 18th is to be found among the general synoptic diagrams.

The winter curves (characterized by short days), represented in fig. 6, which are based upon measurements on January 21st, February 10th and March 19th, are generally marked by lower maxima and more gentle slopes in the morning rise and the evening drop. The average maximum values reach not more than 425 mg/g.h

mg/g.h

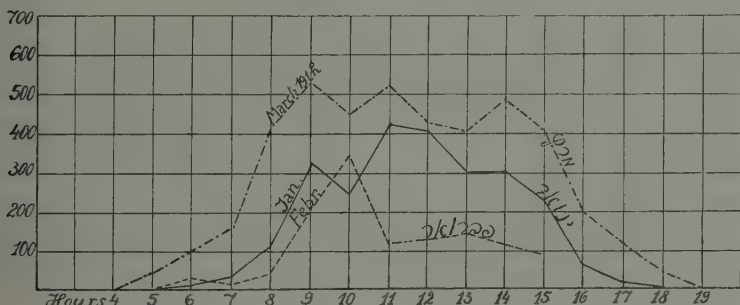


Fig. 6.

The daily march of transpiration in sun light on Jan. 21st, Feb. 20th and March 19th.

in January, 346 in February and 523 in March. It is to be seen that the curves of January 21st and March 19th exhibit a rather regular distribution of the water losses in the morning and afternoon, having summits at 11:00. In the February measurements, transpiration rates in the afternoon were much depressed, owing to increasing cloudiness and humidity of the air. Rain set in at 14:00, and as a consequence measurements were discontinued at 15:00.

In the curve of March 19th, a considerable rise of the general transpiration level is noted, combined with a longer duration of the

daily period of transpiration, as compared with the previous measurements*).

Fig. 7 represents the transpiration in the sun during April, May and June measurements. At this season, the trees were entering the period of complete physiological activity, with increasing length of days as well as temperature of soil and air. Accordingly, transpiration became very intense. After a very steep rise, in the early morning, maximum values were reached as early as 7:00 to 9:00. On May 20th, a khamsin day, values above 1000 mg/g.h were reached by 8:00, and

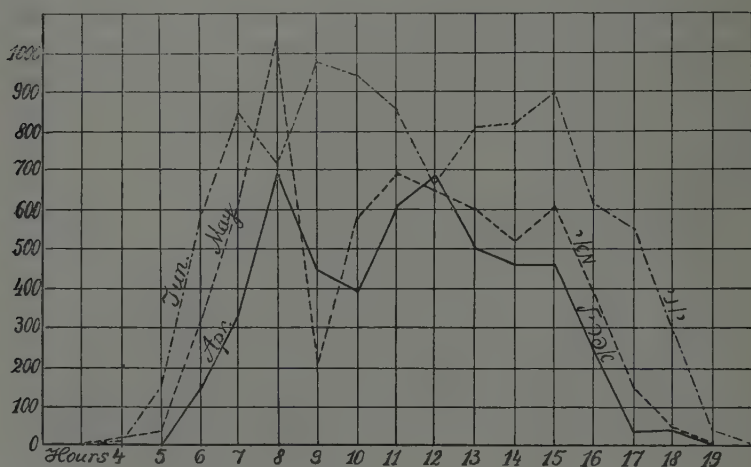


Fig 7.

The daily march of transpiration in sun light on April 21st, May 20th and June 20th.

a restriction of transpiration set in at 9:00. In June, the average rates fluctuated less from hour to hour. This may be considered as an adaptation of the tree to the very regular daily march of climatic factors and the constant high soil temperature and moisture content in the layers of most extensive root development.

The march of transpiration in the months from July to September is represented in figure 8. As typical summer conditions

*) There was extensive root production from March to May. In June, most roots were found to be in a state of rest.

continued with little change, the graphs are hardly to be distinguished from those of the earlier summer months. The only difference is that shorter duration of the day is reflected in a later beginning and an earlier standstill of the transpiration process. The August curve is distinguished, as is the October curve discussed before, by a decrease in values from 10:00 to 14:00, which evidently is here, also, connected with very heavy water losses in the morning hours.

mg/g h

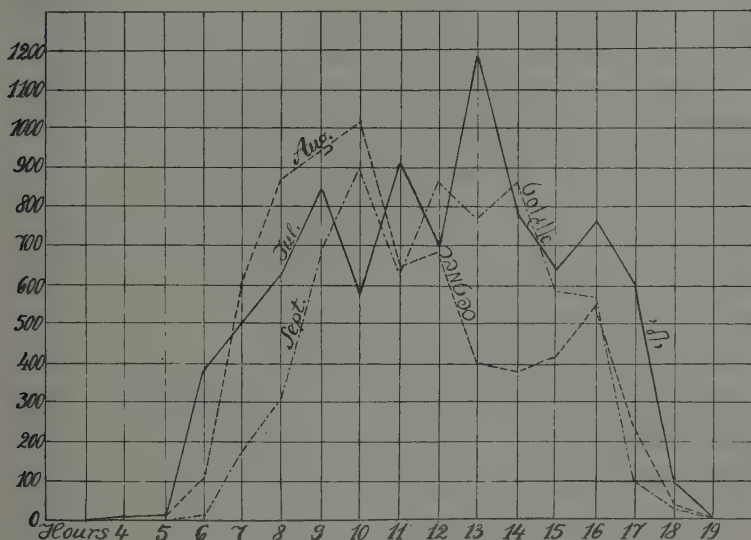


Fig. 8.

The daily march of transpiration in sun light on July 18th, August 21st and September 23rd.

Fig. 9 shows differences in the curves of transpiration on a bright summer and a bright winter day.

2) Transpiration in shade.

The marked dependance of the transpiration process upon intensity of light and sunshine is reflected in the fact that leaves in the shade lose less water than leaves in the sun or in indirect diffuse sunlight. The average ratio of losses in shade and light amounts to about 50%. Ratios were found lower on bright winter days, when shade leaves are more or less inactive than on bright

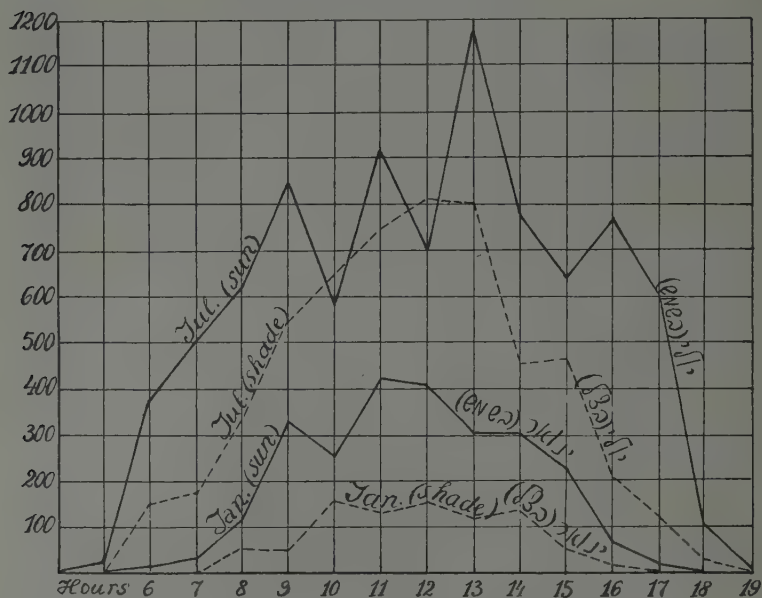


Fig. 9.

Comparison of transpiration in the light and in the shade on a midwinter and a midsummer day.

summer days. This is shown in Table VII computed from planimetric measurements of the area covered by transpiration curves on the respective days.

Table VII.

Total daily transpiration losses of Jaffa orange leaves in the light and in the shade (mg/g.d.).

Date	In light	In shade	Relative losses in shade (light losses = 100)
18/X	6700	3100	46
21/XI	4260	1780	42
18/XII	5140	2010	39
21/I	2550	885	35
20/II	1290	860	67
5/III	2720	1175	43
19/III	4320	2140	50
21/IV	5047	2067	41
20/V	6580	3750	57
20/VI	9620	5270	55
18/VII	8700	5470	63
21/VIII	6538	3975	61
23/IX	6510	3810	58

NOTE: Possibly the shade values, especially those found in the hottest summer months, are somewhat too high. In executing these measurements, we weighed the shade leaves at a short distance from the tree, protecting them with a hat, from the direct radiation of the sun. This artificial shading may have differed, in some respect, from the natural conditions within the crown of the tree. The possibility of a quick reaction of the stomata to the increase in light, as found by BIALOGLOWSKI (8), cannot be absolutely ignored for cases when leaves are transported to a place characterized by different conditions of light and probably, temperature, due to heat radiating from the metallic body of the balance.

It is seen that from October to April, transpiration in the shade was found to be less than 50% of the values in the light. The only exception was February 20th, a cloudy day, when transpiration in the light was so low as to approach the values found in the shade. From May to September, the proportion of transpiration of the shade leaves increased till, in the warmest months, July and August, it reached more than 60% of the transpiration in the light.

In many cases, the daily course of transpiration in the shade resembles that in the light. It seems that the course of the former shows less fluctuations than that of the latter. If this is a general rule, can be decided only after additional experiments. Low temperature and intensity of light are evidently responsible for the reduced activity of the shade leaves in winter. Although transpiration in shade shows the same ascent in the morning and descent in the evening as transpiration in the sun, the smaller fluctuations during the daytime are not always found to run parallel.

III. *Yearly march of daily total losses.*

The values given in Table VII, in view of their considerable theoretical and practical interest, have been represented in figure 10, as columns. It is seen that the entire loss on winter days (January 21st, February 20th, and March 5th) was about 2.5 times the fresh weight of the leaf, in the light, and about the fresh weight, in the shade.

Values rose greatly until on June 20th, the maximum daily loss of 9.62 and 5.27 times the fresh weight in the sun and shade respectively was reached. After that date, the figures again decreased, remaining on a fairly constant level, of about 6.5 times the fresh weight, in the sun, during the autumn months (August to October).

g/g·d

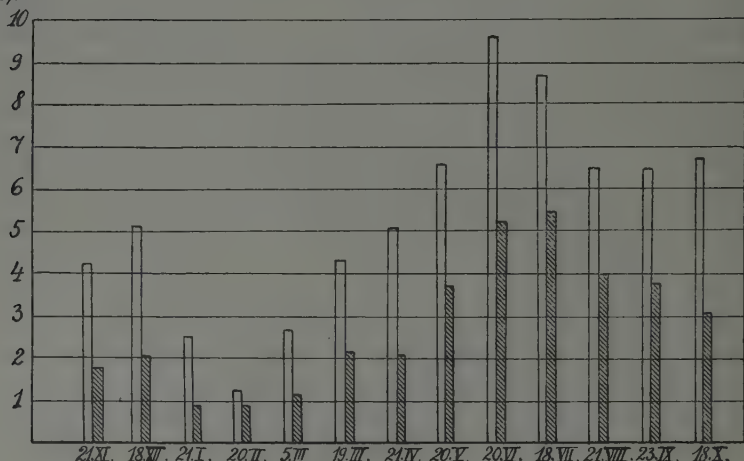


Fig. 10.

The yearly march of Jaffa orange leaf transpiration in sun light (white columns) and shade (hatched columns).

They then decreased further, until a minimum was reached on February 20th, a rainy day, with values that are probably lower than those that would be characteristic of a sunny day of the same season.

Measurements, carried out, for another purpose, in summer, 1937, show, in general, the same amount of daily water loss as in 1934/35.

IV. Transpiration at night.

Whenever the trees were examined before sunrise and after sunset, the stomata were found to be closed, and transpiration practically nil. This proves a remarkable resistance of the cuticle to water loss. As it seemed possible that water might be evaporated on nights, at least during khamsin periods, when the atmosphere is relatively dry, transpiration was measured on the night of October 28th/29th, 1935. 47 weighings were made during this night and all, without exception, rendered values close to zero. The meteorological conditions of this night have been described before (cf. table IV). They were doubtless favourable for transpiration. In view of the fact that 28 leaves tested throughout the night could not be infiltrated by petroleum (only in a few instances were single infiltration spots observed), it may be

concluded that the stomata remained closed throughout the whole night. The very small losses in weight undergone by the leaves are probably to be attributed to cuticular transpiration, which at 22:00 reached a maximal value of 37 mg/g.h and at 4:00 fell to zero (in all five leaves weighed at this hour, not even a loss of half a milligram was recorded in the course of two minutes). This experiment affirms our previous findings (1934) as regards transpiration in the dark. The fact that transpiration is completely stopped, even when external conditions allow the process to go on, is moreover a new contribution to the problem of the effectiveness of stomatal regulation in the higher plants.

V. *Transpiration of young leaves.*

As during our winter measurements, all leaves plucked for weighing belonged to the last two mature growth cycles, we met with no special difficulties as regards the age of the leaves. In spring and summer, however, we were confronted with the problem, already studied by many authors, of whether or not young and mature leaves show a similar intensity of transpiration. Special attention was devoted to this question during our measurements on March 19th, April 21st and May 20th. On the first mentioned date, the young leaves were only about from one to three weeks old and probably physiologically rather inactive, while on April 21st, they were about seven to nine weeks old, fully grown and apparently highly active. They were also very active on May 20th, when they were about 2½ months old.

On March 19th, the transpiration of the young and mature leaves, in the sun, was quite similar. At 8:00 the transpiration intensity of very young shoots, having five leaves and four flowers, was found to be decidedly lower (142—208 mg/g.h) than that of last year's leaves (about 350 mg/g.h), while a nearly full grown young leaf had a still higher water loss (518 mg/g.h). Later, from 10:00 to 15:00, the transpiration of young leaves was found to range at about the average of the older ones. This condition changed markedly at 16:00. At this hour, the transpiration losses of the young leaves were higher than those of the old and, as the infiltration tests also rendered higher figures for the former, it appears that the young leaves did not restrict their stomatal transpiration as quickly and effectively as did the old. At 17:00, when the tree was in the shade, a young leaf still

had a transpiration intensity of 217 mg/g.h, as compared with 70 mg/g.h lost by the mature leaves of the preceding growth cycles.

On April 21st, quite consistent differences in the transpiration of the old and young leaves were established. These are represented in the following table:

TABLE VIII.

Transpiration of leaves of the new spring growth cycle compared with that of the previous year's cycles, on April 21st (in milligrams per gram per hour).

Hour	In the sun		In the shade	
	Spring leaves	Previous season's leaves	Spring leaves	Previous season's leaves
5	0	0	0	0
6	140	159	172	45
7	177	405	117	68
8	498	793	120	104
9	545	398	411	182
10	554	317	516	348
11	727	548	484	110
12	799	629	160	133
13	581	458	464	185
14	518	441	329	88
15	467	461	315	145
16	372	166	146	72
17	46	29	27	25
18	28	43	0	0
Total loss of day	5452	4847	3261	1505

From the table it is seen that at most hours of the day, the losses of the young leaves are much greater than those of the mature foliage. The differences are not so pronounced in the sun, where the total daily loss of the young leaves surpasses that of the mature, by 12%, as in the shade, where the difference is as great as 117%. In the light the young leaves showed higher losses only between 9:00 and 17:00, while in the shade they lost without any exception, more water during all hours of the day.

Infiltration tests, made on the same day indicated that in most cases the stomata of the young leaves have much narrower apertures than those of the mature. This points to the assumption that cuticular

losses are, at least in part, responsible for the higher transpiration values of the young foliage.¹⁾

A higher expenditure of water by the young leaves in the shade was also established on May 20th, the scirocco day mentioned previously. On this day only full-grown young leaves were plucked until 9:00, but afterwards, leaves of the previous growth cycles were also weighed. The differences were still more pronounced than in April as seen in Table IX.

TABLE IX

Water expenditure of young and old Jaffa orange leaves in the shade, on May 20th, 1935 (mg/g.h).

Hour	Young leaves	Previous year's leaves
10	422	156
11	323	145
12	292	57
13	408	142
14	742	116
15	221	199
16	396	286
Total of 7 hours.	2804	1101

It is to be noted that during the hot hours of this exceptionally dry day, young leaves, in the shade, lost 155% more water by transpiration than the foliage of the previous year's growth. As the stomata were found to be nearly closed, for the most part, during these hours, the losses are to be considered as essentially cuticular.

Another series of observations of this kind was carried out on September 29th, 1937. The transpiration in the sun of young (about seven weeks old) and mature leaves was compared between the hours of 7:00 and 16:00. Two leaves of each kind were weighed every hour and the average calculated. In seven out of the ten cases,

*) On March 19th when, on the contrary, very young leaves were found transpiring as much as or less than the mature, between 8:00 and 15:00, it was shown, by means of the infiltration method, that the stomatal apertures of the former surpassed those of the latter. We are unable, so far, to give a satisfactory interpretation of these observations. Possibly the same degree of infiltration established on leaves at different stages of development may not always indicate identical stomatal aperture. On the other hand, the higher relative proportion of plasma and its greater resistance to water loss might explain this behaviour of the young foliage.

the transpiration of the young leaves was found to be greater than that of the old. The total for the above mentioned hours was 7163 mg/g.h for the young leaves and 6587 for the old. i. e. a difference of only 8% in favour of the former. Here, again, the average aperture of stomata in the young leaves was found to be smaller, being 1.3 units, in Schorn's scale, as compared to 2.0 units in the old leaves.

Summarizing the results of our observations, we find that, under the conditions of our experiments, the young Jaffa orange leaves lost, in most cases, more water than the old.

VI. *Proportion of dorsal to ventral losses.*

Experiments were carried out on November 21st, 1934 and on April 21st, 1935 (days of our monthly weighings) in order to elucidate the question which proportion of the total losses of water vapour is to be accounted for by the dorsal and which by the ventral leaf surface. On the first mentioned date, mature leaves were chosen, while on April 21st, young leaves, eight to ten weeks old, of the spring growth cycle, were selected.

The leaves were plucked and the total loss established in the usual manner. After the second weighing, the lower leaf surface was covered with a thin layer of vaseline and the leaf then exposed a second time for two minutes. The first loss was considered as the natural loss of the leaf, the second, as the dorsal loss.

During the investigation carried out on November 21st, 1934, we established figures of dorsal transpiration fluctuating between 4.48% and 18.23% of the total loss. At 8:00 we found 14.10%; at 9:30, 12.20%; at 9:45, 6.24%; at 10:30, 4.48% and at 15:30, 18.23%. A shade leaf, weighed at 10:45, showed a higher percentage than a sun leaf, weighed slightly earlier (7.81% as compared with 4.48%).

Similar results were found on April 21st, 1935. The relative dorsal losses were decidedly higher in the young leaves tested. At this date, we found an average dorsal water loss of 21.39% as compared with an average of 9.01% in the mature leaves examined previously. The dorsal losses on April 21st fluctuated between 10.72% and 36.85% of the total losses. As in November, the percentages in the morning and in the afternoon were higher than in the noon hours. We found 20.05% at 7:00, 17.55% at 10:40, 10.72% at 11:50 and 36.85% at 16:00. In all cases, except the last, sun leaves were measured.

Summarizing the results of these scattered tests, we find:

1. An average dorsal water expenditure of 13.48% of the entire loss was established.
2. The proportion of dorsal to ventral losses is decidedly higher for young than for old leaves. This seems to substantiate the assumption that the cuticular layer of the young leaf is little developed and does not afford the dorsal side of the leaf (which is poor in stomata) a very effective protection from water loss.
3. Dorsal losses are proportionally higher in the morning and in the afternoon than in the hours around noon, when stomatal transpiration (essentially ventral) is at its highest.

VII. *Analysis of water expenditure during the days of observation.*

In the following, we undertake an analysis of the daily march of transpiration in all the curves obtained, as influenced by external factors, on the one hand, and regulations by the plant, on the other. For this purpose, synoptic diagrams have been drawn, which allow comparison of the transpiration curves with those of all the other factors measured.

Meteorological factors are arranged in the upper half of the diagram and physiological processes and indexes, in the lower half. In comparing the curves, it should be remembered that evaporation values are given at the moment in which they were measured, i. e. at the end of each hour. They appear half an hour too late, in the diagrams, as they represent the average of the preceding hour. On the other hand, transpiration measurements were in most cases executed about a quarter to half an hour later than indicated in the diagram. Therefore the reader should mentally shift the whole evaporation curve half an hour to the left and the transpiration values 15 to 30 minutes to the right, if calculations of relative transpiration are to be made. Moreover, it must be kept in mind that there is also a certain lack of correspondence, amounting to 15 or 30 minutes, between the transpiration figures and other meteorological and physiological observations. This causes some difficulties in the comparison of factors such as sunshine, wind velocity and stomatal aperture, which undergo rapid changes.

Transpiration in the light is represented by heavy lines, transpiration in the shade by broken lines, osmotic values by "x"s (x), saturation deficits by crosses (+), and the sun by disks, the blackened part of which designates the degree of covering.

Fig. 11 - 24**Synoptic diagrams of the meteorological and physiological measurements.****1) Symbols :**

Different stages of covering of the sun	:	○ ◐ ◑ ◒ ◓ ◔ ◕ ◖
Soil temperature, at 50 cm	:	□
„ 75 „	:	○
„ 100 „	:	+
Water saturation deficit of the leaves (W.S.D.) — a) mature leaves	:	+
b) young leaves (on March 19th)	:	⊕
Osmotic values	:	×
Transpiration and Stomatal Aperture: Light values	:	—
Shade values.	:	—

2) Abbreviations:

Temp.	=	Temperature
Evap.	=	Evaporation
Sat. Def. Air.	=	Relative Saturation Deficit of the Air
Transpir.	=	Transpiration
CoCl ₂	=	Cobalto chloride values
W. S. D.	=	Water Saturation Deficit of the leaves
Osm. Val.	=	Osmotic values.

3) Measures

Sun covering	:	Degrees 0 — 5
Cloudiness	:	„ 0 — 10
Wind	:	m/sec
Temperature	:	°C
Light	:	Number of relative units
Evaporation	:	cc. (1 cc. evaporation of our evaporimeter corresponds to 1.1 mm evaporation of the usual Piche tubes.)
Rel. Sat. Def. Air.	:	100 — percentage of relative humidity.
Transpiration	:	milligrams per gram fresh weight in an hour (gm/g.h.)
Stomata	:	Additive infiltration values
Cobalto chloride test	:	Percentage of the area turning red
W. S. D.	:	Percentage of deficit in water content at saturation.
Osmotic Values	:	Atmospheres.

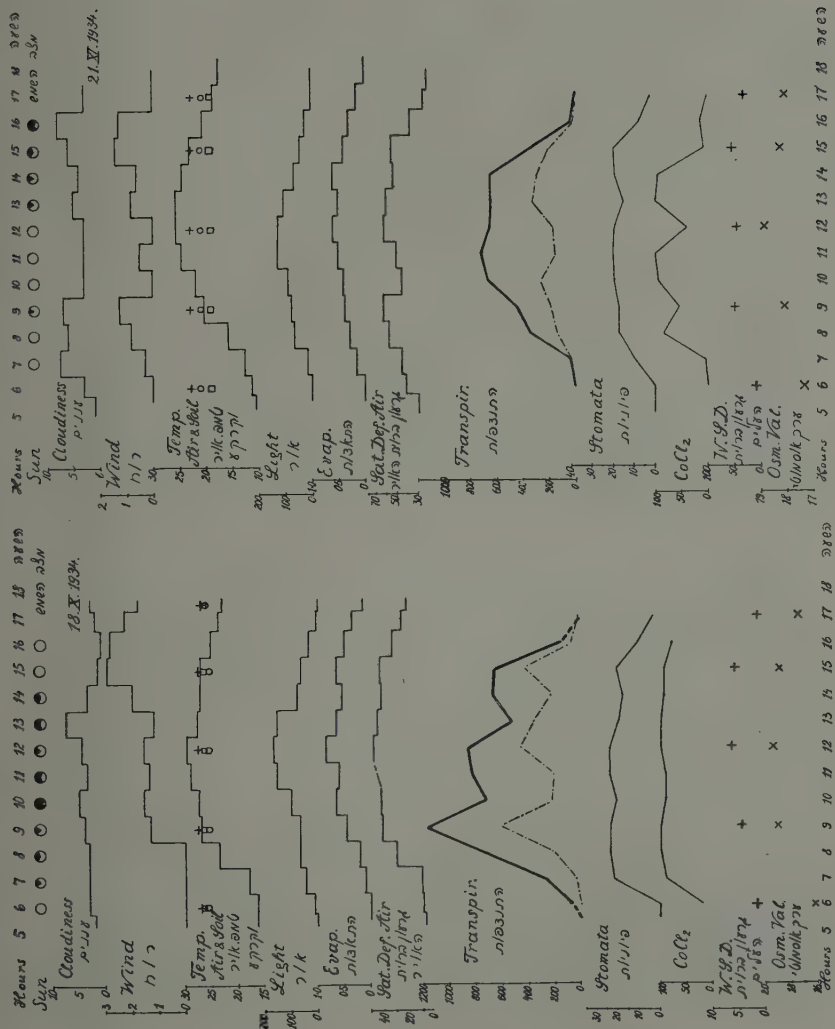


Fig. 11

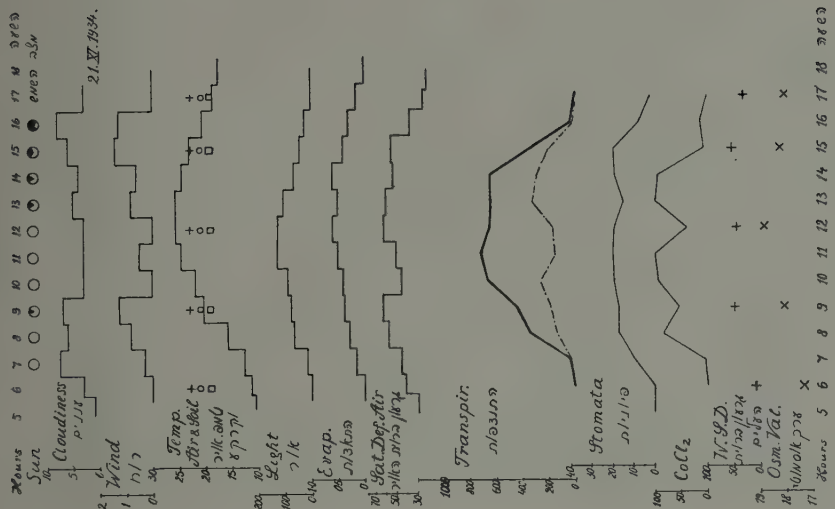


Fig. 12

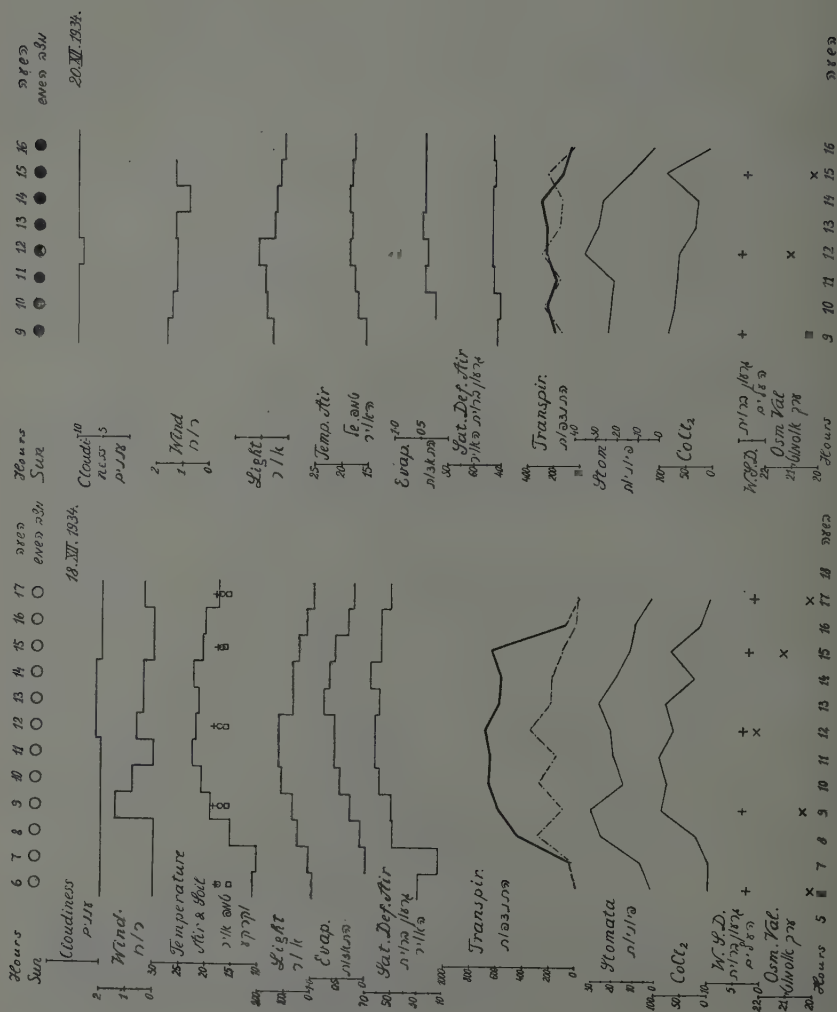


Fig. 13

Fig. 14

Hours 5 6 7 8 9 10 11 12 13 14 15 16 17
Sun

20. II. 1935.

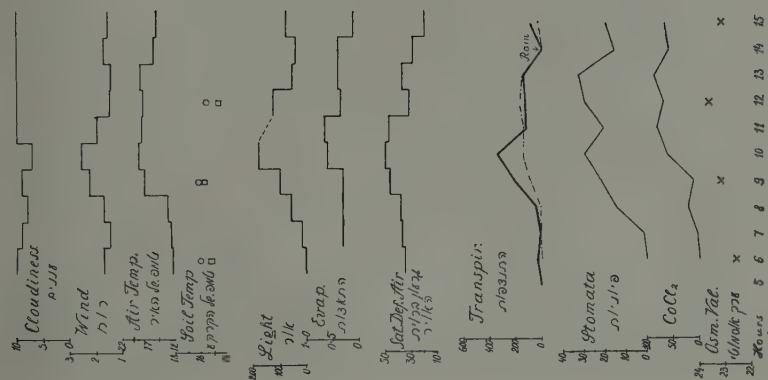


Fig. 16

Hours 5 6 7 8 9 10 11 12 13 14 15 16 17
Sun

21. I. 35

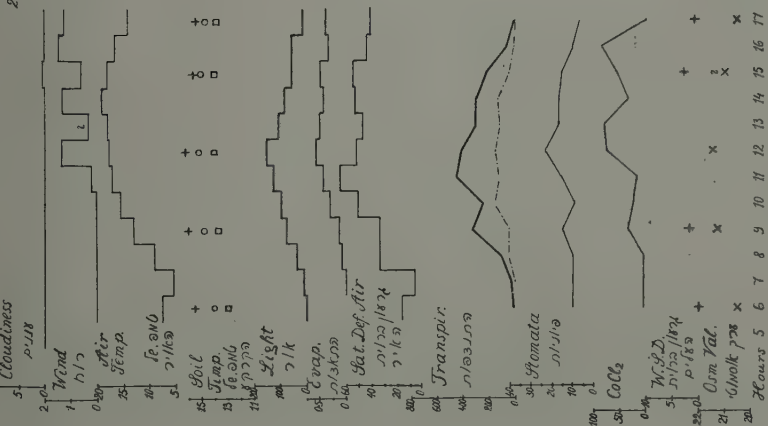


Fig. 15

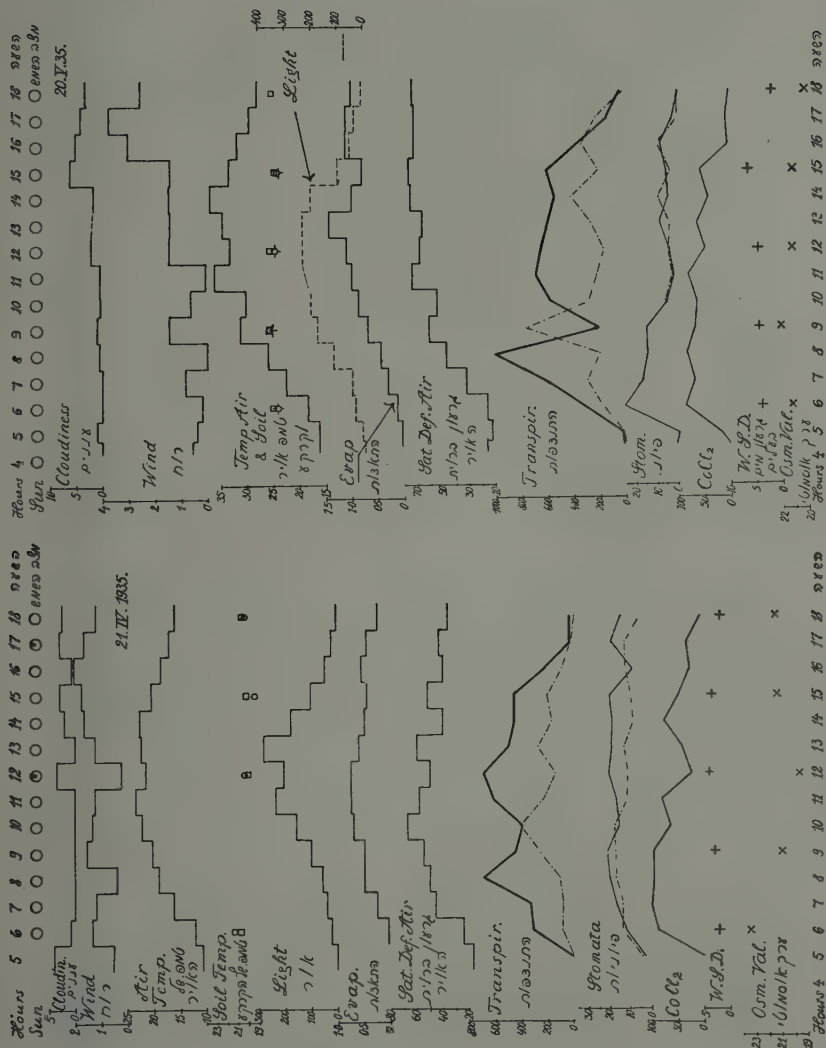


Fig. 20

Fig. 19

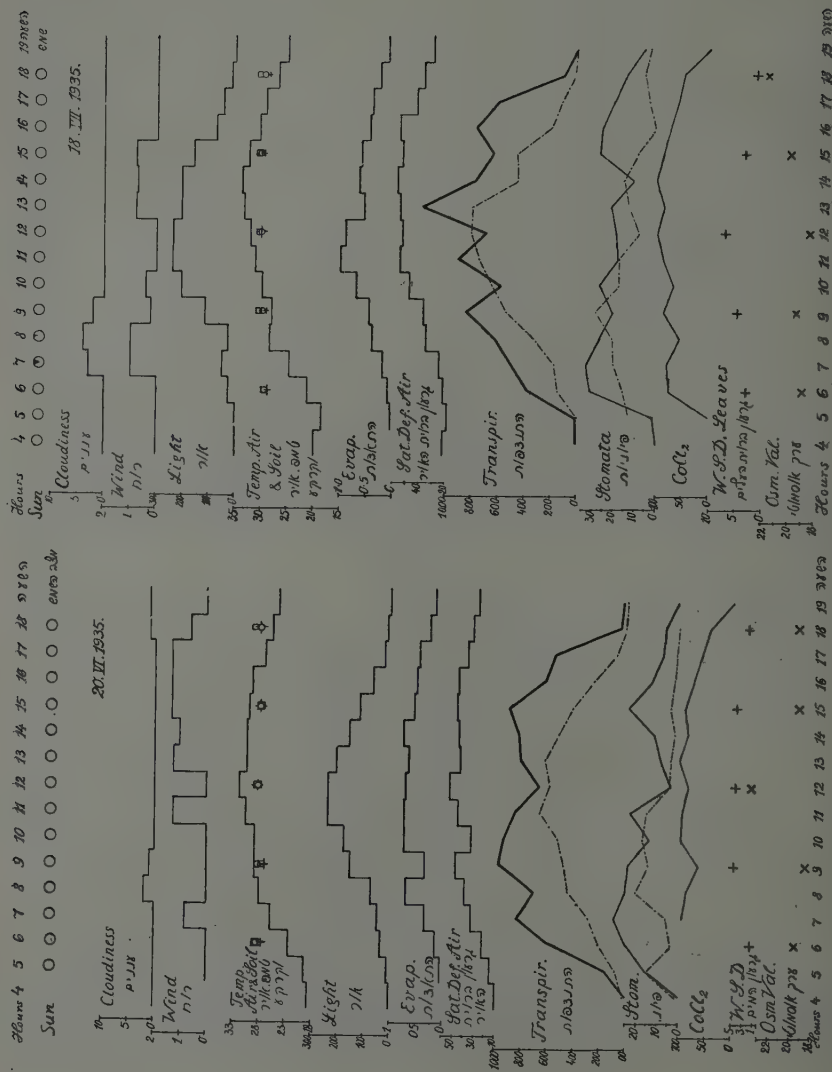


Fig. 22

Fig. 21

October 18th, 1934. (Cloudy day) (Fig. 11). The curves of transpiration in light and shade run parallel to one another and can therefore be discussed together. The steep ascent in the morning coincides with increasing values of all the factors favouring transpiration, in particular, with a steep climb in the temperature of the air (ten degrees within two hours), light intensity and saturation deficit, as well as values designating the degree of stomatal aperture. The relatively heavy clouding out of the sun at 8:00 proved unable to counterbalance this tendency to increase, so that the extraordinarily high figure of 1177 mg/g.h is reached. The restriction of transpiration, following, at 10:00, is to be explained by the increased covering of the sun, which probably leads to a considerable lowering of leaf temperature. At the same time, we find a slight closure of the stomata, which, however, seems insufficient to explain this sharp drop in transpiration intensity. The curve, till 14:00, evidently corresponds to the changes in insolation, and is again reflected in the movements of the stomata. At 15:00 the sky is cleared up and the sun shines unimpeded. Light intensity remains practically undiminished in spite of the decreasing height of the sun. Evaporation intensity and saturation deficit of the air reach maximum values for a last time, with increasing north wind. The stomata again reopen and the intensity of transpiration remains unchanged. Immediately afterwards a steep drop in the transpiration values sets in, produced by the diminishing intensity of solar radiation, which is reflected in closure of the stomata as well as in decreasing figures of evaporation, saturation deficit and temperature of the air. The standstill of transpiration at sunset coincides with the drop of light intensity to zero.

It might be objected that the trend of the transpiration curve can be interpreted in a different manner. For example, the ascent in the morning and the descent in the evening run parallel, not only to light intensity, but also to saturation deficit of the air, evaporation, and temperature of the air. The peak in transpiration at 9:00 coincides with the factors favouring transpiration mentioned above, as well as with the setting in of the daily breeze, and it would seem only natural to insist that these parallel factors explain at least partially the march of transpiration.

Only after a detailed study of a considerable number of such ecological diagrams can it be decided where we have to do with a casual parallelism and where, on the other hand, a causal relationship exists. Such a study has shown that (1) light intensity is the chief and primary factor determining the rise and fall of the transpiration curves in the morning and in the evening, while (2) sun radiation and (3) stomatal regulations are the main antagonistic agents responsible for the fluctuations during the day. We shall, therefore, attempt to explain all of our transpiration curves, principally on the basis of these assumptions.

The water balance of the tree shows evidence of some tension at 12:00, when saturation deficit rises to 6.5%, but is again quite normal in the evening, at 17:00, when the morning value is reattained. The same impression of strain is received from the march of the osmotic values. Soil temperatures are sufficiently high so as not to have any limiting effects.

November 21st, 1934. (Cloudy, dry autumn day, at the end of a six day khamsin period; wind SW to NW) (Fig. 12): The ascent of light transpiration in the morning is slow until 7:00 (sunrise at 6:15), because of the cloudiness of the sky which prevents a rapid increase in light intensity. The transpiration curve rises to a maximum at 11:00 with the increasing light intensity, air temperature and evaporation. The slight covering of the sun at 9:00 seems to have very little influence. From 10:00 to 14:00 the march of transpiration is stable and follows the course of the temperature and evaporation curves. At 13:00 the cloudiness and covering of the sun tend to increase. Transpiration, which might be expected to sink at 13:00, remains stable, but the stomata show a definite reaction in a tangible decrease in aperture. The steady course from 13:00 to 14:00 is accompanied by slightly increased evaporation rates. The rapid fall of transpiration rates at 15:00 is effected as usual by the decrease in light intensity, which is augmented by heavy clouds hiding the sun, and corresponds to the decreasing dryness of the air and to the rapidly sinking rates of evaporation. Cobalt chloride values correspond quite well to the course of the transpiration in light. The curve representing transpiration in the shade follows the course of the relative saturation deficit rather closely, though lagging behind to a certain degree. Whether a causal relationship exists between the drop in the relative saturation deficit at 10:00 and the drop in shade transpiration at 11:00 cannot be decided. The W.S.D. is fairly high at 9:00 and 15:00. This probably indicates a beginning of difficulties in water absorption, owing to low soil temperatures.

A striking meteorological feature of this day is the remarkable coincidence of the values of sun covering, cloudiness and wind velocity associated with the fluctuations of the relative saturation deficit.

December 18th, 1934. (Dry, nearly cloudless day following a rainy period with a precipitation of 100 mm. Winds east and south (Fig. 13): Until 9:00 the steep increase in the intensity of transpiration in the light runs parallel to a strong rise in temperature and dryness of the air and is associated with very wide stomatal apertures. A perceptible, but not very effective reduction of stomatal opening, between 10:00 and 12:00*) is counterbalanced by increasing dryness of the atmosphere. During the whole day, stomatal regulations remain of minor importance, compared with the influence of temperature and humidity, upon which transpiration in the light depends to a remarkable degree. The fluctuations between 13:00 and 15:00 cannot be explained. After 15:00 transpiration sinks rapidly, doubtless under the influence of decreasing light intensity. As temperature and dryness of the air remain on a rather high level, they cannot be held responsible for this drop.

In this day's diagram, we should have expected to find a better correspondence between the values of transpiration and stomatal opening. We wish to mention that a marked inconsistency of the infiltration figures was noted on this date. Great differences in these values were remarked in connection with the insertion of the leaves on different branches. To illustrate this, at 12:00, the

*) The turpentine-castor oil mixture, as well as SCHORN'S liquid III penetrated into most of the leaves tested during these hours.

turpentine-castor oil mixture, as well as liquid paraffin and SCHORN's liquid V penetrated a leaf inserted on a branch facing south-west, while practically all these liquids failed to penetrate (only SCHORN's liquid I seems to have penetrated) a leaf tested on a branch exposed to the southeast (weather side!). Such differences between both branches were found quite frequently in the course of this day. Shade transpiration values being based on one weighing only are not discussed. Quite steady osmotic values and W.S.D. figures give ample evidence of a very good water balance.

Fig. 14 shows the diagram of the incomplete measurement on December 20th, which was already mentioned before (p. 35).

JANUARY 21ST, 1935. (Typical cloudless mid-winter day, winds NE or N): (Fig. 15). The gentle rise of the transpiration curve in the morning is to be explained by the fact that during the night there had been heavy dew, which dried only at about 8:00. The rise until 9:00 corresponds to increasing values of light intensity, temperature and saturation deficit of the air. The minimum at 10:00 is due to stomatal regulations, as root absorption from the cold soil is probably unable to replace (as in warmer months) the water spent by the leaves. The remainder of the curve, till sunset, corresponds remarkably to the courses of the relative saturation deficit of the air and stomatal movements (probably the latter are responses of the plant to the former).

Transpiration in the shade is very weak. Its curve runs parallel to that of the transpiration in the light. At 10:00, however, there is no stomatal restriction, but a rise in transpiration occurs, corresponding to the previous smaller water expenditure.

The influence of the stomata on the whole course of light transpiration, on this day, becomes still more evident, if we compare the curves of stomatal opening and part of the cobalt chloride values with that of light transpiration. All these curves, though differing in details, resemble one another strongly. The curves of osmotic values and W.S.D.'s of the leaves (the value at 12:00 is unfortunately lacking) also correspond noticeably to the course of transpiration. The expenditure of water is easily replaced throughout the day.

The generally low level of transpiration intensity and stomatal opening is noteworthy and corresponds to low temperatures of soil and air.

FEBRUARY 20TH, 1935. (Cloudy late winter day with sun, for the most part, covered and with rather high relative humidity) (Fig. 16): The transpiration course is easily understood if it is compared with the behaviour of the sun. The two peaks, one at 10:00 and the other, a smaller one, at 13:00, coincide with the moments when the rays of the sun pierce the clouds. The minimum, at 14:00, when the curves fall to zero, is caused by rain. Stomatal movements run parallel to transpiration till 11:00. Afterwards, with increasing humidity of the air, the stomata open widely. At 12:00 and 13:00 the stomata are wide open, as the leaves are in optimum water conditions, with sufficient light intensity. The closure at 14:00, is probably due to the decrease in light intensity. Accordingly, stomata reopen at 15:00, when the intensity of light has increased again.

The behaviour of stomata and transpiration from 13:00 to 15:00 allows us to determine whether both processes follow the march of air temperature, saturation deficit or light intensity, in the evening. In the diagram, the close correspondence between the curves of transpiration and light intensity indicates that light is the decisive limiting factor responsible for the closure of the stomata, as was stated previously by other and the present authors.

Incidentally we wish to note that till 13:00 a very close agreement of transpiration is observed with stomatal movements, on the one hand, and with meteorological factors such as temperature, saturation deficit of the air and even wind velocity, on the other. The increase in wind velocity from 8:00 to 10:00 coincides with augmented solar radiation, which seems to be responsible for the decreasing humidity of the air, as well as for the opening of the stomata and the increase in transpiration intensity. With decreasing wind velocity and insolation (11:00—12:00) the effects of these factors are reversed.

March 5th, 1935. (Sunny spring day following scirocco) (Fig. 17): The sky being for the most part unclouded, transpiration is governed by stomatal regulation during the whole day. Because of the dew and high humidity of the air, the morning values are low. At the same time, from 6:00 to 8:00, stomata are rather wide open. The considerably high cobalt chloride values point to the same direction. At 10:00 transpiration reaches a maximum, while stomatal aperture is greatly reduced. This antagonism may possibly be explained by the fact that the sun was behind a cloud at 10:00, leading to decreased stomatal aperture, and shone freely at 10:15, when the transpiration weighings were begun. On the other hand, the fact that stomatal aperture remains on a low level during the next four hours, casts doubt on the validity of such an explanation. Such protracted reduction points, rather, to difficulties in water supply. If this is the case, we may assume that the transpiration figure at 10:00 is produced in the following manner: Reduction of both stomatal aperture and transpiration intensity sets in about 10:00. As is well known, such reductions do not begin at exactly the same time in all leaves and branches, and it is easily understood that agreement cannot always be expected during transition periods.

Between the two peaks at 10:00 and 14:00, both transpiration rates and figures of stomatal opening are low. The descending slope of the transpiration curve, from 14:00 to 17:00 is governed, as always, by the decrease in light intensity. The midday depression of transpiration is clearly antibatic* to the saturation deficit and evaporation curves (the latter to be shifted to the left, cf. p. 42).

The generally low level of the transpiration curve is to be explained by the low temperature of air and soil.

*) "Symbatic": from Greek *συν* : together and *βαίνο* : to march and "antibatic" are terms used by German authors in referring to the parallel or inverse course of two curves.

March 19th. (Bright, dry, warm spring day with moderate scirocco conditions) (Fig. 18): The sudden rise in the transpiration figures, in the morning, is provoked by the rapid increase in air temperature and the extraordinarily steep rise of the saturation deficit of the air. The depression at 10:00 is easily explained, as decreasing insolation, together with a further rise in saturation deficit and an unusual increase in evaporation, give rise to a stomatal restriction of water expense. This is followed by a second increase in transpiration at 11:00, which is symbatic with stomatal aperture and antibatic to the march of the saturation deficit of the air and evaporation.

From 10:00 to 14:00, each value in the light transpiration curve is the average of two very diverging figures. The dry, warm conditions of the atmosphere impose a marked strain upon the water balance of the tree, which is reflected in the high water saturation deficits of the young leaves as shown in the diagram.

Certain leaves and branches show losses corresponding to the atmospheric conditions, while others react by restricting their water expenditure. The transpiration figures measured were: 330 and 608 mg/g.h at 10:00, 608 and 472 at 11:00, 220 and 632 at 12:00, 542 and 214 at 13:00 and 647 and 302 at 14:00. The figures of stomatal opening were found to be much more consistent. At any rate, no close agreement between transpiration figures and stomatal opening can be expected under such conditions, and it is not surprising to note that a rise in the transpiration curve at 14:00 coincides with a depression in the stomatal and cobalt chloride values. Later, lower transpiration values are caused by decreasing figures of light intensity and possibly by lowered temperature of the air. The covering of the sun from 16:00 onwards contributes to the tendency of the transpiration figures to decrease.

Transpiration in the shade corresponds, in general, to the course of the evaporation curve. It is easily understood that the peripheral leaves, which are subject to the extremes of atmospheric conditions may restrict their water expenditure, while the shaded leaves, within the top, respond to the more favourable microclimatic conditions without undergoing stomatal regulations.

April 21st, 1935. (Bright, rather cool spring day with west winds of varying velocity) (Fig. 19): As there was no dew on the leaves in the morning, the transpiration in the light sets in with a very steep ascent accompanied by increasing, but rather low stomatal values. This sharp rise leads to a high peak of transpiration as early as 8:00. The drop following at 9:00 cannot be explained, as external factors, as well as stomatal behaviour, would seem to favour a further increase of the losses. The minimum at 10:00 coincides with a reduction of stomatal aperture. The rise between 10:00 and 12:00 is effected by increasing values of stomatal aperture, which show a course antibatic to the march of the saturation deficit. The slight and transitory covering of the sun at 12:00 has no influence upon the transpiration process. From 12:00 to 15:00 restrictions by the plant are suspended and transpiration follows evaporation till 15:00, when the evening drop begins.

Transpiration in the shade shows a course quite different from that found in the sun. Throughout the day, we find a remarkable parallelism between transpiration and stomatal movements in the shade. The same parallelism prevails between the shade transpiration and the saturation deficit of the air during the whole day. The different reactions of the leaves in the light and in the shade produce a very sharp contrast between their respective transpiration curves. Their courses are antibatic between 8:00 and 13:00. The difference in the intensity of the strain imposed upon the leaves in the light and shade respectively is obvious from the fact that the first peak in transpiration in the shade is reached (after a very gentle rise) an hour later than in the sun.

The water budget is easily balanced by the tree, as seen from the rather low figures of the saturation deficit. Soil temperatures of about 21°C. are probably still below the optimum [BIAŁOGŁOWSKI (10) found 25° to be optimal for the absorption of Sour Lemon cuttings] .

May 20th, 1935. (Very hot scirocco day of late spring) (Fig. 20): After a night without dew, transpiration in the light rises very steeply from 5:00 to 8:00, following the extraordinary increase in light intensity, temperature and saturation deficit of the air. The stomata are wide open at 6:00, but reduction in aperture immediately sets in. This, however, seems insufficient to explain the remarkable drop at 9:00, when leaves in the light expend only 20% of the water lost one hour earlier. In spite of the nearly hermetic closure of the stomata, from 10:00 to 12:00*), transpiration in the light rises again to considerable values, corresponding to the water expenditure of ordinary days. These losses are due essentially to cuticular transpiration, threatening the epidermal tissue with desiccation. In spite of the closure of their stomata the leaves are forced to follow the courses of temperatures, saturation deficit and evaporation, which reach extraordinarily high figures. The drop in transpiration figures after 15:00 may be explained in part by the fall in temperature. Moreover, there is a possibility, that, with decreasing light intensity, a remnant of stomatal transpiration is done away by additional closing of the stomata.

Thus transpiration intensity drops to figures close to zero (41 and 49 mg/g.h respectively) at sunset, although the temperature of the air is still as high as 27.6°C., the saturation deficit of the air not less than 73% and a strong dry wind is blowing!

Transpiration in the shade takes a very different course, reaching its first maximum at 9:00 and following stomatal regulations for the rest of the day. The parallelism between transpiration and stomatal movements is ideal in this case. While transpiration in the sun follows the rising saturation deficit, evaporation and temperature, the fluctuations of transpiration in the shade are opposed to the courses of these factors. Comparing this behaviour with conditions in our April measurements, we find in both cases antibatic courses of light and shade

*) At 11:00 petroleum and xylene were found unable to penetrate, or penetrating only to a very small degree, corresponding to conditions at night.

transpiration. There exists, however, a fundamental difference. In April shade transpiration runs parallel to meteorological factors, while transpiration in the sun shows a reverse behaviour in the morning hours. In May, when both light and shade transpiration undergo sharp stomatal restrictions, shade transpiration is inverse to meteorological factors (due to successful regulation) while sun transpiration runs parallel to them owing to the inability of the stomata to prevent considerable total (cuticular) losses. Notwithstanding the very extreme atmospheric conditions, we find that the tree balances its water budget quite successfully, as seen by the W.S.D. values, which do not surpass 6.9% (at 15:00) and sink as low as 2.4% at 18:00. *The total daily loss is not greater than is to be expected for an average day of the season.* (Fig. 10). On the other hand it may be understood that a long duration of such conditions can, so to speak, break the wall of cuticular and stomatal resistance and kill all or part of the leaves, especially if there is insufficient water in the soil.

June 20th, 1935. (Typical cloudless early summer day) (Fig. 21): Weather conditions are at this date quite ideal for the Jaffa orange tree as the temperatures of air and soil are high, and there is abundant light and sufficient humidity of the atmosphere.

The sun being uncovered throughout the day, transpiration in the light seems to be governed, primarily, by stomatal regulations. From 4:00 to 7:00 the water expenditure follows, as usual, the march of atmospheric factors and runs practically parallel to the curve of stomatal opening. As early as 8:00 the first restrictions of transpiration are observed. The degree of stomatal opening decreases, transpiration becoming antithetic to evaporation. From 9:00 to 15:00 transpiration is restricted by increasing closure of stomata, leading to a sharply defined minimum at noon when the stomata are nearly closed. Restrictions by the plant are suspended more and more until 15:00, when a third maximum is attained. The sharp drop of transpiration in the evening follows a similar drop in light intensity (the decrease in air temperature and saturation deficit seems insufficient to account for the sudden fall between 17:00 and 18:00).

As in other instances of very heavy water expenditure, there is a pronounced inconsistency between the transpiration and infiltration values from 10:00 and 13:00. Some leaves are found to restrict transpiration, while others do not. Thus at 12:00 one leaf loses only 435 mg/g.h while the other loses 915 mg/g.h. At 13:00 one leaf is infiltrated both by petroleum and xylene to the velocity degree of III, whereas another is found to have its stomata nearly closed; so that xylene is unable to penetrate. Under these circumstances no parallelism between stomatal behaviour and transpiration from 10:00 to 11:00 could be established.

Remark: The curve of transpiration in the shade shows a marked lack of correspondence with the course of the stomatal movements and follows, instead, the curves of temperature and light intensity. This unusual lack of agreement between stomatal aperture and transpiration values arouses suspicion as to the accuracy of our measurements under midsummer conditions. In the

hours of the most marked differences between the two curves, the sun stands high in the heavens at an angle of 60° to 80° . It seems that the intensity of light is very low in the shade at such times, the difference between figures of light intensity in shade and light being extraordinarily great. As already pointed out (cf. "Transpiration in shade" p. 39), there exists a possibility of strong instantaneous stomatal movements when transferring the leaves to conditions of greater light intensity. For this reason it might be suspected that our values for shade leaves were too high in our midsummer measurements.

It must be added, however, that weighings carried out in August, 1937 with the transpiration balance placed in the shade within the top of the tree close to the stem again rendered, in many instances, high transpiration figures (500—800 mg/g.h) associated with low infiltration values. The latter were, in this case, established for the same leaves which had just been weighed. This seems to disagree with the explanation given above for the said disproportion, and suggests that the values established are quite reliable. Possibly under the meteorological conditions of the Palestinian summer, stomatal aperture must become very small before a strong reduction in transpiration is produced.

July 18th, 1935. (Typical, nearly cloudless, bright midsummer day) (Fig. 22): The steep ascent of the curve from 5:00 to 6:00 becomes more moderate between 6:00 and 8:00. This can be explained by the partial covering of the sun, or rather by the slow decrease in humidity. As early as 8:00 a slight restriction of the stomatal aperture sets in, which is not effective in reducing transpiration. (Paraffin oil penetrates most leaves throughout the day). Thus transpiration in the light continues to increase until 13:00, showing, however, considerable fluctuations which cannot be explained by the course of the meteorological factors: temperature, saturation deficit and evaporation. Only at 14:00, when the curve of stomatal aperture sinks very low, does restriction become noticeable. At this time a considerable W.S.D. seems to have been established in the leaves (the figure at 12:00 reaches about 7%). At 15:00 stomata are again wide open and at 16:00, with the degree of aperture unchanged, transpiration reaches a last peak of 769 mg/g.h. The drop from 16:00 to 19:00 corresponds well to the decrease in light intensity and stomatal aperture.

Shade transpiration follows stomatal movements from 5:00 to 9:00 and again from 14:00 to 16:00. The disproportion between transpiration and stomatal aperture observed in June and discussed above, is found on this day only in the hot hours between 9:00 and 15:00. During this interval the external factors appear to have a much stronger effect on the process than stomatal restrictions, which seem, in this case, quite ineffective.

August 21st, 1935. (Typical, almost cloudless, late summer day). (Fig. 23): The ascent of the curve of transpiration in the light is delayed until 6:00, as the sun is hidden by clouds. Afterwards, as there are no changes in insolation, transpiration in the light as well as in the shade is found, with few unimportant deviations, to follow stomatal movements. The stomata of leaves exposed to the sun are wide open from 7:00 to 9:00. A sharp reduction in stomatal aperture

sets in later followed at 11:00 by a corresponding decrease in transpiration rates. Thus quite low transpiration values are found at 13:00. Afternoon transpiration is slow in following increasing rates of stomatal aperture. This can be explained by the high moisture content of the air, especially pronounced at 15:00. The peak at 16:00 corresponds to increased rates of saturation deficit and evaporation. With values of light intensity below 50 relative units, transpiration rates sink close to zero at sunset.

It is to be noted that stomatal movements from 8:00 to 15:00 and transpiration rates from 10:00 to 15:00 are strictly antitactic to the curves of temperature and relative saturation deficit. As evaporation rates are quite moderate at the same time, so that a rather symbiotic course would be expected, we are led to the conclusion that the very considerable loss of water in the morning hours created a high saturation deficit in the leaves which it took several hours to fill. Indeed, the values of saturation deficit of the leaves correspond quite well with the course of transpiration, showing a decided drop only after the sharp restriction of stomatal aperture at 13:00. Moreover, possibly the conditions of the water supply were not as favourable on this day as intended in the plan of the investigation. It may be that the irrigation (by artificial rain) did not saturate the soil, and this may have been responsible for the slow reestablishment of the moisture content of the leaves. In support of this assumption, it may be added that later measurements with insufficient soil moisture rendered similar curves.

The remarkable agreement between the curves of transpiration in the shade and the corresponding stomatal movements is worthy of special emphasis. The restriction of stomatal aperture in the shade is pronounced only between 9:00 and 10:00. Afterwards the courses of stomatal movements and transpiration become roughly symbiotic with the course of the saturation deficit of the air.

September 23rd, 1935. (Typical late summer day, cloudy and sunless in the morning hours, clearing up later on) (Fig. 24): Morning transpiration in the light is very small in view of the high humidity of the air, covered sun and heavy clouds. At the same time stomatal aperture (the stomata beginning to open at 6:00 at a light intensity of only 17 relative units) reaches very high figures. Between 8:00 and 9:00 the sky clears up and air humidity decreases. As a consequence evaporation evidences a sudden rise. Transpiration rates climb at once to considerable values, reaching a first peak as late as 10:00. Now, following the increase in the saturation deficit of the air, moderate stomatal regulation sets in leading to a drop in transpiration intensity at 11:00. At 12:00, however, stomata again open a little wider and consequently a second peak of transpiration is reached at 12:00. Transpiration intensity remains at this level till 14:00. The intensity of transpiration at this hour stands in sharp contrast with the results of the stomatal infiltration measurements. At 15:00 transpiration decreases considerably corresponding to a sharp drop in the saturation deficit of the air. The definite decrease in transpiration rates after 16:00 is, as always, to be explained by a photic reaction of the stomata to decreasing light intensity.

The water balance being favourable the whole day long, stomatal regulation is moderate and the only retarding effect on water expenditure worth mentioning is observed at 11:00. Consequently the transpiration course of the day is governed by meteorological factors, principally by the course of the saturation deficit (showing a striking correspondance with the march of transpiration!) and the temperature of the air. Cobalt chloride values correspond rather well to the course of transpiration in the light. The W.S.D. of the leaves corresponds roughly to the march of transpiration.

Transpiration in the shade resembles that in the light and both strictly follow stomatal movements till 9:00 and after 14:00. Between these hours transpiration and stomatal movements exhibit courses antitatic to one another, as observed in the former months.

The conditions of this day are quite similar to those of the July measurement. The high figures of transpiration in the afternoon correspond to increased evaporation values at that time, which agree, in turn, with increasing wind velocity. The essential point in the explanation of the two curves, however, may probably be sought in the fact that morning transpiration had been moderate and no extraordinary strain had been laid on the water balance of the tree in the early hours of the day. Soil temperatures are still rather high and favourable for the absorption of water by the roots.

Conclusions.

The analysis of the daily transpiration graphs of sun leaves leads to the conclusion that there was a regular march of transpiration, without fluctuations, during winter days (November 21st and December 18th) when no sudden and strong changes in insolation interfered (as happened on February 20th and October 18th). This also holds true for March 19th, when however, there was a drop, due to covering of the sun associated with an important reduction in stomatal aperture at 10:00.

The situation on January 21st, March 5th, April 21st, May 20th, June 20th and August 21st was quite different. On these days the fluctuating course of transpiration was governed primarily by stomatal regulations. In all these cases we must suppose that the water balance of the tree was under a strain provoking effective hydroactive reduction of stomatal aperture. This tension was caused by low temperature of the soil on January 21st and March 5th, and by heavy water losses, especially in the first hours of the day on the late spring and summer dates.

The diagram of September 23rd shows the effect of both external and internal factors. External conditions played an important part, with stomatal restriction evident at 11:00. It is difficult to interpret the curves of April 21st and July 18th, probably because of drawbacks in our methods.

E. DISCUSSION.

In the following we shall discuss some facts established in the course of our investigations and compare them with findings of other authors who dealt with the transpiration of plants in general or citrus transpiration in particular.

The daily march of transpiration. Our statement that losses at night are very small and in many cases negligible corresponds to the observations of BARTHOLOMEW (6) for citrus trees and of BRIGGS and SHANTZ (16), MAXIMOW (48, p. 151—153) and STOCKER (75, II) for other plants. BARTHOLOMEW (6), working with Valencia orange leaves, established that night transpiration reached maximum values of about 100 milligrams per square decimeter per hour in the second growth cycle and only about 40 milligrams per square decimeter in the fourth cycle. These figures agree quite well with our findings. As a square decimeter of the Jaffa orange leaves used in our measurements weighs on an average about three grams, our maximum figure of 37 milligrams per gram found on a dry scirocco night is equivalent to about 111 milligrams per square decimeter. In other words, our figures fluctuated within the same limits as those of BARTHOLOMEW. The restriction of transpiration at night was found to be connected with a closure of the stomatal pores, corresponding to previous statements of OPPENHEIM (51) and the present authors (53) for Jaffa oranges, and of many authors for other species [as LOFTFIELD'S (47) for onion, corn and cow-beet]. BIALOGLOWSKI (8), working with Eureka lemon cuttings, also found differences in the intensity of transpiration in the light and in the dark that agree with our findings. Investigating the march of transpiration in a 24 hour period, with a temperature of 30°C. and 89% humidity, he found a transpiration figure of 3390 mg. for 12 hours in the light, while during an equal period in the dark, only 65 mg. were expended. In other words, transpiration in the dark, in this case, represented less than 2% of the total loss. At other temperatures and humidities the

relative losses in the dark were somewhat higher, but as table 4 of the cited work shows, transpiration in the dark rarely exceeded 5% for old and 10% for young growth.

Hitherto there has been little study of the march of transpiration in citrus leaves, during the day, using reliable methods. The steep increase of losses in the morning and the equally steep decrease in the evening, recorded by us, correspond to findings of BARTHOLOMEW (6) and BIALOGLOWSKI (8). Fluctuations occurring during the day may be understood as the product of the many changes of external conditions and stomatal regulations and, therefore, require no further discussion.

At times our transpiration curves show two peaks. Similar curves were, to the best of our knowledge, first described by EDITH SHREVE (67), who counted for them by a disproportion between water expenditure and supply in the morning hours. Our April, May and August curves are essentially of this type. In the May curve there was a pronounced "ultramaximum" in the morning followed by a corresponding deep fall in transpiration intensity. The theory explaining such two peaked curves was further developed by STALFELT (70) and STOCKER (75, III).

Triple apex curves are found in our diagrams: on the khamsin days (December 18th, March 19th, May 20th) and on all days of measurement during the summer (from June to October). They are considered by EVENARY and RICHTER (22) as characteristic for transpiration under desert conditions.

The absolute losses. The losses per hour established by us are quite comparable with those found by other workers, using the same method with other plants. BOSIAN (13), studying the transpiration of various perennials and shrubs of the xerophytic Kaiserstuhl flora in Southern Germany, found maximum values, ranging between 481 mg/g.h (*Teucrium montanum*) and about 1680 mg/g.h (*Artemisia campestris*) on July 24th, 1931, which compare remarkably well with our maximum values. HAERTEL (34), working under similar conditions on the Frauenstein near Vienna, found, in midsummer, maximum figures of 1500 mg/g. h. for *Orithantha lutea* and *Sanguisorba minor*, values which closely approach our maxima for citrus. Miss HOFMANN (35) also working on the Frauenstein, found, on hot days, losses far

surpassing ours. She recorded 2373 mg/g.h for *Potentilla arenaria*, 2750 for *Sanguisorba minor* and as much as 3099 for *Cynanchum Vincetoxicum*.

Transpiration experiments carried out by STOCKER (75) between the arctic zone and the equator rendered again quite comparable results. As STOCKER published figures based on units of surface, we must transfer them to the fresh weight basis by multiplying STOCKER's figures with the *surface: fresh weight* ratio published by this writer in order to facilitate such comparisons. By such calculations, we find that STOCKER's *Rhododendron lapponicum*, at Abisko (68°21'n. lat.) at noon on June 26th lost 405 mg/g.h, when the temperature of the air was 13°C. and the relative humidity 66%. Under exactly the same conditions, on January 21st, 1935, at 9:00, we found an average figure of 330 mg/g.h for our comparable citrus leaves, which comes quite close to STOCKER's value.

Comparisons with STOCKER's trees in Hungary seem less admissible: *Populus alba*, tested in the Hungarian black alkali steppe (Hortobagy puszta) rendered on June 8th, 1929, at 10:25, a figure of 1260 mg/g.h, which closely approaches the loss established by us for citrus on October 18th. at 9:00. The external conditions of this day corresponded roughly to our October and November conditions, the temperature fluctuating at the hours compared in the vicinity of 25°C. and the humidity around 55%.

Results of weighings made by STOCKER at BUITENZORG. (Java) with evergreen leaves of *Calophyllum inophyllum* and *Elacodendron glaucum*, on November 26th, 1929, are quite comparable with those of Jaffa orange leaves under our conditions in June. *Calophyllum* lost, on this day, 650 mg/g.h at 8:05 (27°C., 67% humidity), while Jaffa orange leaves, in our experiments, lost 710 mg/g.h at 8:00 on June 20th (28°C., 61% humidity). *Thus it would appear that leaves of a similar structure have similar rates of transpiration at the polar circle as well as at equatorial latitudes, if atmospheric and soil moisture conditions are comparable.* This matter is recommended for further studies.

No data, quite comparable to ours, on the hourly losses of orange leaves are to be found in the literature. BARTHOLOMEW (6), working in the orchard with lemon and orange leaves, in the shade of a cheese-cloth, attached glass shells, filled with calcium chloride, to

both sides of the leaves. In this manner, he determined the transpiration of definite leaf areas, with a moisture deficit of 100% of the air in the shells. BARTHOLOMEW notes that these tests were not meant to establish, "actual amounts of transpiration", but were undertaken for other purposes. Nevertheless, a comparison of his figures with ours is of interest. BARTHOLOMEW, on one day of his measurements, between 9:00 and 12:00, found in Valencia orange leaves, an hourly loss of about 670 milligrams per square decimeter, equal to about 225 mg/g.h, if we suppose that one square decimeter of his leaves weighed 3 grams. Such a rate of transpiration corresponds only roughly to our figures established in the shade, in the months of BARTHOLOMEW's measurements (July to October). The fact that BARTHOLOMEW's figures are on an average somewhat lower than ours might be explained either by differing external conditions or by a reduction of stomatal aperture, which may possibly have occurred during his measurements, as was the case in BIALOGLOWSKI'S (8) tests, made in low humidities. BARTHOLOMEW (6), himself, states (p. 776)," that in some cases the conditions of the test appeared to cause the stomata to close partially". Under these circumstances, the fact that our figures are somewhat higher than BARTHOLOMEW's, may be understood.

The daily totals of transpiration losses, in our experiments vary between 1.3 and 9.6 grams per gram of fresh weight. Within these wide limits, we can easily include v. HOEHNEL'S (36) figures, found in Vienna, for *Betula verrucosa*, which lost, in his experiments, according to this author's calculations, 1.87 grams per gram fresh weight in a day, as an average of the entire vegetation period. An average of 3.13 grams is given by this writer for the three hottest months of the year, while on very hot summer days, the daily loss would, according to v. HOEHNEL'S estimations, be five or six times greater than the latter figure. This might be somewhat exaggerated, for it indicates figures considerably higher than the transpiration losses of the Jaffa orange leaves on the hottest days of the Palestinian summer.

HOFMANN (35) gives the following daily losses for various plants on extremely hot August days (near Vienna): *Teucrium montanum* 4.5 grams, *Helianthemum canum* 8.1 grams, *Globularia cordifolia* 9.2 grams and *Onosma Visianii* 7.6 grams. These losses

are quite comparable with those we established in our summer measurements. BOSIAN'S (13) totals even slightly surpass ours. This worker recorded for *Artemisia campestris* 10.2 grams and for *Helianthemum chamaecistus* 11.3 grams. STOCKER'S (75, II) daily totals established for trees, on summer days in Hungary, similarly are quite high as compared with our figures. In a strong wind, he found the daily losses for *Populus virginiana* to amount to 7.8 grams, for *Populus alba* to 14.1 grams (!) and for *Elaeagnus angustifolia* to 13.1 grams per gram fresh weight in a day. EVENARI and RICHTER (22) recorded in the Judean desert maximum values for the following plants: *Haplophyllum tuberculatum* 26.9 g, *Reseda muricata* 21.9 g, *Heliotropium rotundifolium* 15.2 g, and *Erodium glaucophyllum* 14.7 g. per gram fresh weight in a day.

In order to compare our findings with those of previous European and modern American writers, we must calculate our own figures on the basis of surface units. As mentioned above, approximate values for the losses of our leaves per square decimeter are obtained by multiplication of the figures indicated in Table VII by three. In this manner, we obtain the following values for sun leaves: February 3.9 grams, March 13.0 grams, April 15.1 grams, May 19.7 grams, June 28.8 grams and July 26.7 grams per square decimeter of surface (one side of leaf) in a day. These figures seem very high in comparison with those established by PFAFF (56; 3.6—5.7 grams), in his research on the transpiration of an oak tree in Bavaria, as well as in comparison with those of other early writers [HABERLANDT (30), MUELLER (50)] who found values ranging between one and six grams per day. A much higher figure was, however, established by UNGER (76) for *Helianthus annuus*, which on August 25th lost 17.22 grams per square decimeter per day.

v. GUTTENBERG (27), studying surface losses of Mediterranean macchia shrubs, found, in potometer experiments, daily losses ranging from 4.2 (*Quercus Ilex* in spring) to 10 grams (*Pistacia Lentiscus* in summer). Maximum values were established for *Rhamnus Alaternus*, the old leaves of which transpired 20.8 grams in summer and for *Cistus* species, (*C. villosus*, *C. monspeliensis*), where figures surpassing 30 grams were found in summer. These, however, are considered as somewhat too high by the author himself, as it was difficult to determine the uneven leaf surfaces

accurately. At any rate these figures are similar to those of our June and July measurements. Still higher figures of surface transpiration *tuberculatum* 83.4 g, *Reseda muricata* 47.5 g, *Heliotropium rotundituberculatum* 83.4 g, *Reseda muricata* 47.5 g, *Heliotropium rotundifolium* 40.8 g and *Erodium glaucophyllum* 32.0 g per square decimeter in a day !

There are relatively few indications as to the water loss of citrus leaves in 24 hours. HAAS and HALMA (29) published figures for small citrus cuttings cultivated in a *green-house* at Riverside, California. The daily losses per square decimeter of the lower leaf surface only, amounted, in August, to 1.66—3.89 grams per day, and are apparently much lower than our figures.*) BARTHOLOMEW (6), working during the late summer months at Riverside, does not publish daily totals, but it seems that the transpiration intensity found by this worker, amounting to a few grams per square decimeter per day, is also considerably lower than our midsummer findings.

Much higher figures were established by BIALOGLOWSKI (8) in his thesis. The daily losses of his Eureka lemon cuttings at 30°C. and humidities ranging between 40 and 70%, amounted to 2.50—5.40 grams per square decimeter per day, for one year old growth. Still higher losses were established for growth of the current season, where water losses, under the same conditions, rose as high as 15.80 grams per square decimeter per day, a figure corresponding to our April measurements (cf. Table 14, p. 73 of BIALOGLOWSKI's thesis). We do not think it surprising that our maximum losses far surpass even BIALOGLOWSKI's, as trees rooted naturally in a well aerated soil probably have a much more intensive water metabolism than small cuttings cultivated in aqueous solutions as were those which were used by HAAS and HALMA (29) and by BIALOGLOWSKI (8). It should be kept in mind that our figures were established under extraordinarily favourable moisture conditions of the soil.

The transpiration of young and mature leaves. This general problem has been investigated by many authors who have

*) When these cuttings were tested under outdoor conditions, the daily losses were about the same as indoors. In Marsh grapefruit and Valencia orange, they were even considerably smaller. It must be remarked, however, that plants transferred to outdoor conditions do not render values comparable to those of plants accustomed to growing outdoors, as restrictions of water expenditure are liable to set in.

reached very inconsistent conclusions. BURGERSTEIN (17), in his monograph (p. 58—62), summing up the information available on the subject at the beginning of this century, was inclined to suppose that young leaves transpire to a stronger degree than old, founding this impression on the researches of v. HOEHNEL (36), AUBERT (5), N. J. C. MUELLER (50) and others. Since then many modern authors as BERGEN (7), v. GUTTENBERG (27), KAMP (42), REED and BARTHOLOMEW (61), CARTELLIERI (18), BARTHOLOMEW (6), MONTEMARTINI (49), SCHMUCKER (62) and others, have worked on the same problem in the course of their studies.

From a study of their papers, one finds that the majority of the modern writers arrive at the conclusion that mature leaves lose more water than young. This was established by BERGEN (7) and v. GUTTENBERG (27) for evergreen Mediterranean species, by KOKETSU (44) for *Coleus Blumei* (with the exception of the youngest leaf), by S. KEEBLE (43) for *Amherstia*, by CARTELLIERI (18) for species of *Rhododendron* and *Vaccinium* and by SCHMUCKER (62) for *Fagus*, *Tilia*, *Brownea Ariza*, species of *Coffea*, *Abies* and *Picea*. For *Citrus* trees, this view is supported by BOEUF and GENET (12), REED and BARTHOLOMEW (61), and BARTHOLOMEW (6).

A higher transpiration, on the contrary, by young leaves was found by PISEK and CARTELLIERI (59) for *Cynanchum Vincetoxicum* (probably for leaves of the same growth cycle), in some cases by KAMP (42) for the youngest leaves of *Elatostemma sessile*, by SCHMUCKER (62) for the youngest leaves of species of *Quercus* in midsummer, and by MONTEMARTINI (49) for *Myoporum serratum*, especially in diffuse daylight. BIALOGLOWSKI'S (8) work with citrus trees is to be mentioned in this connection. He found that cuttings from the current season's growth transpired much more per square decimeter of leaf surface than cuttings from one year old growth (Table 14 of the cited work).

Needless to say, different results will be obtained in such experiments in accordance with varying external conditions and inner regulations by the exposed plants or plant organs. Leaves called "young" by BERGEN (7), were one year old, whereas the "old" leaves of *Fagus*, *Tilia* etc. studied by SCHMUCKER (62) were only a few months old. Moreover the various growth cycles of trees compete with one another for water, and if interchanges of water between the

growth cycles are not excluded under the conditions chosen by the experimentalist, no consistent results can be expected. If we assume [what most authors except KAMP (43) admit] that the young leaf has higher cuticular and lower stomatal losses than the old, and that the stomata open wider with advancing development of the leaf, we arrive at the conclusion that we are concerned with a very complicated problem which deserves a special fundamental study under well defined conditions.

Interpreting our own results, which agree with those of BIALOGLOWSKI (8), rather than with findings of the other authors, it appears that a Jaffa orange leaf, before it is fully grown, loses under moderate external conditions, an amount of water comparable to that expended by the previous growth cycle. When the leaves of the spring cycle are two or three months old, they are very active and lose, in the warm hours of the day, more water than the previous year's growth. Restriction in the evening, through closure of the stomata, takes place more slowly than in the older leaves (April 21st). While the greater losses during the warm hours of the day are, to a considerable degree, cuticular, the slower decrease of transpiration intensity of the young leaves in the evening can be explained only by stomatal regulation. The question as to why differences between transpiration losses of young and old growth were found to be so much more pronounced in the shade than in the sun gives rise to further difficulties. Possibly the previous year's leaves, plucked in the shade, had to be taken from places where light intensity was generally low. Consequently the regulative capacity of these leaves (destined to drop before long) might have been restricted, explaining the small stomatal aperture and consequent small transpiration figures. We feel, however, that this explanation is rather doubtful, especially as the results of our infiltration tests are contradictory. The fact that young leaves in the shade were found to transpire so much more actively, as compared with the mature leaves, than was the case with young leaves in the sun is in itself of considerable interest.

On the whole, our experience seems to substantiate findings of earlier writers [v. HOEHNEL (36), N. J. C. MUELLER (50), cf. BURGERSTEIN (17), I, p. 58—59], indicating that in the course of development, the transpiration intensity of the leaves undergoes regular changes which can be explained by decreasing cuticular and

increasing stomatal transpiration. If this is the case, a maximum of transpiration is to be expected at the stage when cuticular losses are still considerable and stomatal expenditure has already reached a high level. This probably held true for the young leaves in our April measurements.

Dorsal versus ventral losses. The fact that stomatal regulation plays an essential part in citrus transpiration is again brought out by the results of the study of dorsal and ventral losses. Our results correspond quite well to those of BARTHOLOMEW (6), who worked with Navel and Valencia orange varieties. It seems of interest, therefore, to compare our figures with those of BARTHOLOMEW. Weighing orange leaves at about noon, the following proportions of dorsal to total losses were found under orchard conditions:

Shamouti: old leaf 6.15%; young leaf 14.14% (Compare also OPPENHEIMER and MENDEL) (54);

Navel, old leaf 6.50%; young leaf 9.19% (BARTHOLOMEW) (6);

Valencia, old leaf 10.20%; young leaf 12.4% (BARTHOLOMEW) (6).

Just as BARTHOLOMEW and v. GUTTENBERG (27) (the latter working with evergreen Mediterranean shrubs), we found the proportion of cuticular transpiration higher for young than for old leaves. BARTHOLOMEW's figures as given in table 2 of his paper, fluctuate less than ours. Perhaps this may be explained by the fact that the "mature" leaves used by BARTHOLOMEW were, as a matter of fact, the lowest leaves of the previous growth cycle. We, on the other hand, designate as "mature" leaves about five months old.

Our results disagree with those of KAMP (42). This writer, investigating the proportion between dorsal and total transpiration for leaves two and 14 months old, taken from the same plants, found, in most cases, higher dorsal (cuticular) losses for mature than for young leaves.

The influence of external factors:

Light. — We have come to the conclusion of previous authors who studied the transpiration of plants that light is a factor of paramount importance in orange leaf transpiration. It can exert

an influence, either direct or indirect, through the mediation of the stomatal apparatus. On the other hand, radiant light energy can affect the plant directly or as diffuse sunlight. In the former case, much of the light energy is often transformed into heat and it is difficult to determine whether the rise in transpiration is effected by photic or thermic influences.

There can be no doubt that the rise of transpiration in the morning and the decrease in the evening, which takes place whether the sky is clouded or not and in rather low light intensities, is produced essentially by *photoactive* stomatal reactions.*) In this respect our study confirms earlier statements by OPPENHEIM (51), BARTHOLOMEW (6), BIALOGLOWSKI (8) and the present authors (53) on the behaviour of citrus stomata. In our experiments, stomata opened quite widely when light intensity, in the morning reached about 50 relative units and closed again when it fell below this level. We, therefore, agree with LOFTFIELD (47, p. 50) who stated that during the bright hours of the day, light is supraoptimal as a factor governing stomatal movements: "Changes in light intensity have no observable direct effect if they occur above 50% of the maximum for the region, but produce corresponding changes in stomatal movement in many plants growing where the light is less than 10%".

During the noon hours we find that the light does not assume an important rôle unless it appears in the form of direct solar radiation, which has been justly referred to by MAXIMOV (48) as the "principal factor regulating the rate of transpiration". Our statements that transpiration reacts immediately to the increase and decrease of solar radiation on cloudy days agree with STOCKER'S (75) recent observation, in the Hungarian steppe, and with v. GUTTENBERG'S (27) findings for Mediterranean shrubs (p. 398). (See also EVENARI and RICHTER (22), graph 1 and 4, pp. 349/50).

Information as to the heat produced in citrus leaves by insolation is to be found in the results of measurements, published quite recently by BODENHEIMER (11). The purpose of these measurements was to study the body temperature of scale insects inhabiting the

*) We do not however deny the possibility that the "passive" and "hydro-active" systems of STALFELT (72) may play some part in the opening in the morning and the closure in the evening, as shown by this author in other cases.

citrus leaves. Since, however, the thermocouple used by BODENHEIMER was inserted into the body of the scale insect through the opposite side of the leaf, his figures are probably representative of the leaf temperature also. At Rehovot a "leaf-insect" temperature of 29.4°C . was established, in the sun, as an average of 66 measurements carried out on October days, this being as much as 10.8°C . higher than the average temperature of the air in the shaded centre of the top of the tree. Moreover, the published graphs show clearly that the combined leaf-insect temperature follows a course quite different from that of the air and that shading by clouds or leaves causes a quick drop of leaf temperature, in comparison with that in the bright sunlight. According to BODENHEIMER, scale insect bodies (leaves) would be considerably warmer than the surrounding air even in the shade. At Rehovot, an average difference of 5.3°C . between the two temperatures was established in 67 measurements. It is difficult to understand how these differences in the shade can be explained. They may possibly be produced by heat reflected from the soil? The differences of temperature established by BODENHEIMER are higher than those found by SCHRATZ and FRITZSCHE (64) and approach maximum figures found by various other authors (cf. HUBER, *Waermehaushalt der Pflanzen*, Muenchen, 1935).

Aside from the thermic effect of radiant energy, it seems quite possible that light exercises a specific influence on the permeability of the plasma to water, which might in turn be responsible for rising transpiration figures. In this connection, we wish to mention BRAUNER's recent investigation (15), in which he tested tissue cylinders, taken from the root of *Beta vulgaris*. The velocity of expansion of such cylinders in solutions was accelerated markedly after exposure to light. This proves according to BRAUNER's opinion, that light increases the permeability of the protoplasm to water. While, according to BRAUNER (15), this can be explained by a diminution in the electronegative charge of the outer cell layers, owing to the loss of electrons, F. CHODAT (19) assumes that the light, or, to be more exact, the ultraviolet part of the spectrum activates the sterols at the periphery or in the interior of the cytoplasm. Thus a complex, with physiological qualities resembling those of vitamin D, is formed which in turn mobilises calcium and thus influences the degree of swelling and permeability of the protoplasm.

Whatever may be the true nature of these still rather problematic effects of light on permeability, which are discussed by CHODAT (19) in connection with transpiration, it is easy to understand that the escaping water vapour will be more readily replaced by water molecules from the interior of the mesophyll cells if the resistance to their diffusion through the outer plasma layers is diminished. On the basis of our experiments, we are unable to decide whether changes in plasma permeability played any important part in the transpiration of our orange trees.

SORAUER (68), incidently, had already stated that light, independent of thermic influences, increases transpiration. The later discussion on this subject by LECLERC DU SABLON (45) and others is reported by MAXIMOV (48). MONTEMARTINI (49) stated that in the laboratory, diffuse light greatly increased the transpiration of *Myoporum serratum*.

Other external factors. — A glance at the synoptic tables is sufficient to show that there is apparently a considerable degree of correlation between temperature and transpiration intensity. Humidity also corresponds markedly to transpiration, in agreement with findings of BIALOGLOWSKI (8). On the other hand, there seems to be little correlation between water expenditure and wind, though the influence of wind in increasing stomatal as well as cuticular transpiration seems well established by the researches of FIRBAS (24), STALFELT (71) and WRENGER (81). This picture of the relation of the external factors to transpiration agrees quite well with the opinion presented by MAXIMOV (48) in his book (p. 156). HALMA (32, p. 276) confirms the finding that even strong hot winds do not necessarily cause a marked increase of water expenditure of orange trees. Investigating a grove of Washington Navel oranges, this author found that the influence on the water balance of the leaves of a temperature of 117°F. with humidity as low as 14% was insignificant in comparison with that produced by the lack of available water in the soil. This rather surprising feature can be explained only by an effective regulative capacity of the citrus leaf, which we have again established in this study.

Relative transpiration. — Just as SEYBOLD (66) we feel certain that calculations of relative transpiration based upon the water loss of evaporimeters are of limited value especially if the shape of

the evaporimeter differs from that of the plant organ compared. Nevertheless, some correlation between the losses of the *Piche* evaporimeter and the citrus leaves does exist, as our synoptic tables show. Often strong departures are associated with stomatal restrictions while other deviations cannot be explained, but may be understood in principle in view of the fact that blotting paper is affected differently by wind and radiation than the leaf. The fact that our trees were investigated under favourable moisture conditions, doubtless increased the correlation coefficient. When we tried to plot transpiration losses against the evaporation values of our *Piche* tube, we failed to find a pronounced linear relation between both as was the case in the experiments of PISEK and CARTELLIERI (59).

Stomatal regulation. Interpreting the dependance of the daily march of our transpiration curves upon stomatal movements, we find, that within the range of relatively wide apertures, the changes in stomatal opening were ineffective. On the other hand, they proved efficient when the degree of aperture sank as low as 5 or 10 of our scale, i. e. in most cases when turpentine-castor oil and paraffin oil did not penetrate. Such behaviour agrees with the laws established by STALFELT (72) for the dependance of diffusive capacity upon the degree of stomatal aperture.

F. SUMMARY.

The daily and yearly march of Jaffa orange leaf transpiration was studied in a typical citrus region under orchard conditions. Six year old trees, budded on Sweet Lime stocks, were kept under *optimal water conditions*.

The method adopted consisted in rapid weighings of detached single leaves with HUBER's transpiration balance. This method is discussed critically and historically. Once a month measurements were taken every hour from dawn to sunset. At the time of the weighings meteorological records (solar radiation, degree of cloudiness, temperature of air and soil, humidity, wind velocity and evaporation (*Piche* tube) and physiological observations (stomatal behaviour, osmotic values of the leaf sap and water saturation deficit of the leaves) were made. The manner in which these observations and measurements were made, together with their results are discussed in detail.

Transpiration losses were found to increase steeply after sunrise, reaching, in most cases, a first peak three or four hours later. These values fluctuated in the hours around noon, and later a decided drop towards zero sets in three or four hours before sunset. Night transpiration was found to be very small, reaching zero even in a scirocco night. The daily graphs have been arranged according to seasons and are given in figures 5 to 8.

Maximum values attained in the various seasons show a strong dependance upon climatic conditions. We found average maxima of transpiration in the sun reaching 300 milligrams per gram of fresh weight in an hour in December, 489 in March, 975 in June and 867 in September. Extraordinarily high figures were attained on July 18th 1935, at 13:00 and on October 18th 1934, at 9:00, when 1705 and 1792 mg/g.h respectively were measured. As water comprises about $\frac{2}{3}$ of the weight of orange leaves, this means a water loss of about 2500 milligrams per gram of water per hour. In other words, all the water contained in the leaf is expended and has to be replaced within 24 minutes, if this intensity of transpiration persists.

The daily totals of transpiration losses in the sun and in the shade are given in Table VII and figure 10. Transpiration in the shade rendered values about one half as great as those found in the sun. Sun leaves lost 1.3—2.5 times their fresh weight per day in winter, 4.3—6.5 in spring; 6.5—9.6 in summer and 4.2—6.7 in autumn. In most cases, young leaves were found to lose more water than mature. The loss of the lower side of the leaf was found to be appreciably higher than that of the upper. On November 21st, 1934, dorsal losses in the morning and evening reached 10 to 20% of the total transpiration, while during the period of strongest transpiration, in the morning, the share of dorsal cuticular losses sank as low as 4.5 to 8%.

Transpiration losses on scirocco days were not found to be much higher than losses corresponding to the general conditions of the seasons, while evaporation, during the daytime, on such days was found to be about 60% higher than normal. This was true even of a very hot and dry scirocco day in May, characterized by rather unusual atmospheric conditions.

The observations demonstrate a remarkably effective regulative capacity of the orange leaf and explain the fact that this

species can be cultivated under the atmospheric conditions of a semi-arid climate. Stomatal regulation plays a paramount part in the mechanism of restriction of excessive water losses.

An analysis of the fluctuations found in the daily transpiration curves, shows that light intensity, insolation, and humidity of the air strongly influence the march of the process, while wind velocity is of less significance. The stomatal regulations, governed, on the one hand, by light and on the other by the water balance of the leaves, are in most cases responsible for the deviations of transpiration from the course of the evaporation curve, occurring, for the most part, during the hot hours of the day. *In this respect, we arrive at the same conclusions as STALFELT while our analysis of the influence of external factors agrees with the results of BRIGGS and SHANTZ.*

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AN ANATOMICAL STUDY OF THE FRUIT-BODY OF THE WOOD-ROTTING FUNGUS *Ganoderma lucidum* (Leys.) Karst. IN PALESTINE

BY I. REICHERT AND ZEHARA AVIZOHAR

Division of Plant Pathology, J. A. P. Agr. Res. Sta., Rehovot.

(With Plates XI—XIV and 1 Text-figure)

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I. INTRODUCTION

Ganoderma lucidum, as indicated elsewhere (27), causes serious damage to various trees including important fruit trees grown in Palestine, such as species of orange and stone-fruit trees. The pathogene, however, can frequently not be identified as it appears only in its mycelial form and does not always produce fruit-bodies. The mycelium of *G. lucidum* is then difficult to distinguish from the mycelia of other wood-rotting fungi occurring in this country, and especially from *Ganoderma applanatum* (26). Other criteria must therefore be sought to ascertain the identity of the pathogene.

The best means to this end is the comparative study of the hyphal components of the fungi under discussion, from the commencement of their growth until the formation of the fruit-body, and the detailed description of their distinguishing characters. As a first step in this direction this paper describes the results of an anatomical study of the fruit-body of *Ganoderma lucidum* which will elsewhere be compared with *Ganoderma applanatum*. A study of the parasitizing mycelia of these two fungi will follow later.

The anatomical study of Polyporaceae has long been neglected by mycologists, and this fact has recently been stressed by prominent students of this group of fungi (7, 24). Of recent times only isolated studies covering the whole anatomical structure of a member of the Polyporaceae are known to us. GAEUMANN in 1928 (16) and JACZEWSKI in 1933 (20), both of whom made comprehensive surveys of the literature on the morphology and anatomy of fungi, in the case of Polyporaceae only mention the anatomical studies of RICHARD FALCK. BOSE (7) reviewing the literature on Polyporaceae in 1936 has only one name, that of CORNER, to add to the earlier surveys.

FALCK was in fact the first among modern mycologists who carried out detailed investigations into the anatomy of various Polyporaceae. His most important findings have been included in his two monumental monographs on *Lenzites* (14), published 1909, and on *Merulius* (15), published 1912. We were unfortunately unable to obtain the monograph on *Lenzites* to which direct reference can therefore not be made. Some of the data contained therein are however quoted in the monograph on *Merulius* and were thus indirectly available to us. In the latter monograph FALCK gave a

detailed description of the hyphal systems and their interrelations as observed in *Merulius*. He first described the generative hyphae (termed by him "Bildende Faeden") which he recognized to give rise to the hymenial layers. Among other types of hyphae he described in detail the skeletal hyphae (which he termed "Plattenfasern" or "Faserhyphen") and, as we shall see later on, discussed their interrelations with the generative hyphae.

More recently CORNER (12, 13) has published two papers fundamental for the anatomical study of the Polyporaceae. In these papers a minutely detailed description of the hyphal elements and their interrelations is coupled with an extraordinarily clear and competent exposition of the problems involved. CORNER coined the internationally acceptable terms Generative and Skeletal Hyphae for the hyphal types previously met with in FALCK'S study, and described them in every detail. Incidentally, mention may be made of the fact that JACZEWSKI (20) called FALCK'S "Faserhyphen" by the name of "sclerenchymoidal hyphae", but CORNER'S term "skeletal hyphae" appears far more suitable and should therefore be maintained.

MATERIAL AND METHODS

Our investigations were carried out on dry specimens of fruit-bodies of *Ganoderma lucidum* found on the following six hosts: *Prunus Amygdalus*, *Ceratonia Siliqua*, *Eucalyptus* sp., *Morus alba*, *Prunus domestica*, *Olea europaea*, and *Citrus sinensis* (orange) budded on Sweet Lime. All our results were verified on all the specimens.

The microscopic sections were made by hand, using mainly dry and untreated material. On a few occasions the material was placed into alcohol before the sections were made.

Observations on unstained material were carried out on sections mounted in lactophenol or glycerine. Sections of the crust were mounted in glycerine, as this is the only way to preserve the laccate resinaceous layer of the crust intact. This laccate layer dissolves in lactophenol but not in glycerine; the section must however not be heated, or else this layer will dissolve even in glycerine.

In order to distinguish between the different types of hyphae we used two stains: ordinary Cotton Blue stain and Leischmann's

stain, introduced by BOSE (6), which we further improved by additional differentiation with acetic acid or lactophenol.

Staining sections with Cotton Blue we followed the usual procedure and heated them slightly. Staining with the improved Leischmann's stain was carried out as follows:

1. A drop of Leischmann's stain is placed on the section made from dry material and is left for half a minute.
2. One to two drops of distilled water are placed on the section and left for five minutes.
3. The section is washed with distilled water.
4. The section is differentiated very rapidly with acetic acid or lactophenol, and is then washed quickly with water.
5. The section is mounted in glycerine and is then ready for observation. The stain persists for at least a few months.

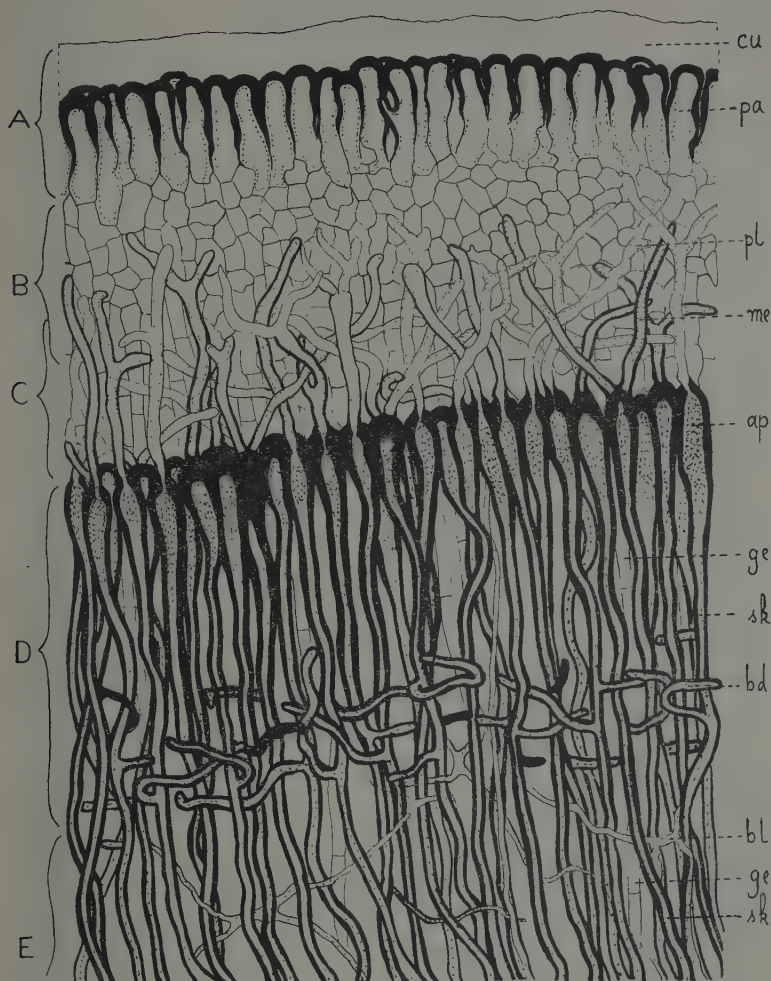
The slide must be washed thoroughly with distilled water before staining.

BOSE (6) who first used ordinary Leischmann's stain undifferentiated by acetic acid or lactophenol for staining sections of *Ganoderma lucidum*, states that in the brown species of *Fomes* the basidia stain violet, while the hyphae of the trama stain green. We carried out similar stainings with *Ganoderma lucidum* but obtained green staining in the palisade layer only, whereas the hyphae of the trama stained violet. With our improved method all plasmatic hyphae (generative hyphae, plasmatic ends of skeletal hyphae), and lumina of palisade hyphae etc. stained pinkish, while the walls of palisade hyphae stained green.

THE HYPHAL SYSTEMS

For the better understanding of the histological structure of *Ganoderma lucidum* all the fundamental elements, the hyphae, composing the fruit-body will in the following be described in detail.

Each kind of hyphae is concerned with the construction of a histological system with a special physiological function. In the enumeration of the various kinds of hyphae we agree with CORNER (13) in not classing them after their origin but according to their common function. Hyphae of common origin may happen to have entirely distinct functions.



TEXT-FIG. I.

Diagram of the structure of the outer portion of the fruit-body.

- A. Palisade layer: *cu*, laccate cuticle, *pa*, palisade.
- B. Plectenchyma.
- C. Layer of plasmatic, *pl*, and mediate, *me*, hyphae with characteristic terminal ramifications forming a binding system.
- D. Dark belt: *ap*, dark swollen apex of *sk*, skeletal hyphae; *bd*, binding hypha of dark belt; *ge*, generative hypha.
- E. Light belt: *sk*, skeletal hypha; *bl*, binding hypha; *ge*, generative hypha.

I. SKELETAL SYSTEM

(a) *Skeletal hyphae*

Compose the bulk of the fruit-body and occur in all except its youngest growing zones. Branched or unbranched, cylindric, aseptate, mostly straight or slightly flexuous, seldom kinked, $2-6\mu$ (majority $3-4.5\mu$) wide, with dark yellow-brown walls measuring $0.75-2\mu$ in width, and narrow lumen which is partly obliterated in the older stages of the more proximal zones. At the distal end of each zone the skeletal hyphae are dark, swollen, becoming more or less club-shaped and thick-walled, $3-9\mu$ (majority $6-7.5\mu$) wide. (Text-fig. 1 sk; Pl. XI, fig. 3 d, Pl. XIII, figs. 9, 10). Unstained by Cotton Blue and stained deep olive-green by improved Leischmann's stain.

(b) *Plasmatic hyphae*

Occur only in the outmost marginal zone of the upper and lower surface of the fruit-body, where the crust has not yet developed, and at the young margin. Branched or unbranched, cylindric, aseptate, bright yellow or colourless, $1.5-5.5\mu$ wide. Intertwining and slightly thickened at their proximal, generally thin-walled at their distal ends which may or may not be tapering or swollen. Represent the initial stage of the skeletal system. (Text-fig. 1 pl; Pl. XII, fig. 7). Lumen stains strongly blue with Cotton Blue, pinkish with improved Leischmann's stain.

(c) *Mediate hyphae*

Occur usually in the 2-3 zones immediately inside the zone of plasmatic hyphae, between the latter and the zones of skeletal hyphae, especially while the margin is young. Under a mature crust they are found even in the outmost zone. Seldom unbranched, mostly profusely branched and interwoven, cylindric, aseptate, yellowish-brown, $1.5-6\mu$ (majority $3-4.5\mu$) wide, walls slightly thickened. Slightly swollen at the distal end of each zone. Represent the intermediate stage of the skeletal system and serve as binding hyphae near the crust and tubes (Text-fig. 1 m; Pl. XI, fig. 3; Pl. XII, fig. 4 c, 5). Lumen stained blue with Cotton Blue or weakly pinkish with improved Leischmann's stain, while walls stain greenish with the latter.

2. GENERATIVE SYSTEM

Occurs in the 2-3 marginal zones on the upper and lower surface of the fruit-body. Particularly noticeable in the young grow-

ing margin. Mostly unbranched or seldom branched, cylindric, septate, straight, longitudinal, $2-6\mu$ (majority $3-4.5\mu$) wide, hyaline, very thin-walled, very seldom with clamp-connections. (Text-fig. 1 ge, Pl. XII, fig. 4 d). Stained very weakly or not at all by Cotton Blue, pinkish by improved Leischmann's stain.

3. BINDING SYSTEM

(a) *Binding hyphae of the dark belts*

These occur only in the proximal portions of the well differentiated dark belt of each zone. Generally thick-walled, dark brownish, aseptate, $2-6\mu$ in width, running at approximately right angles to the skeletal hyphae (Text-fig. 1 bd; Pl. XIII, figs. 8, 10). Staining reactions like those of skeletal hyphae.

(b) *Binding hyphae of the light belts*

Occur chiefly in the light belts, run obliquely and in all directions across the skeletal hyphae, intertwining with them and with each other. Pale yellow, aseptate, $0.5-2.5\mu$ wide, with slightly or fairly thickened walls (Text-fig. 1 bl; Pl. XIV, fig. 12). Mostly stained bluish by Cotton Blue.

(c) *Binding hyphae near the crust and tubes*

Occur where the ends of the zonal arcs approach the crust and tubes. Comprise mediate and plasmatic hyphae. Profusely branched and intertwined, particularly dense near the tubes, while skeletal hyphae grow in a more or less longitudinal direction. Cylindrical, aseptate, yellowish, $1.5-6\mu$ (majority $2.5-4.5\mu$) wide, slightly thickened. (Text-fig. 1 C; Pl. XI, fig. 3; Pl. XIV, fig. 11). Those near the crust are stained bluish by Cotton Blue, pink by improved Leischmann's stain.

4. PALISADE SYSTEM

Occurs in the outer part of the crust. Unbranched, generally aseptate, rarely septate in their lower part, $35-50\mu$ long. At their distal end they are $7-13\mu$ wide, very thick-walled, resembling basidia, with narrow lumen. the walls measuring at the apex $3-4\mu$ below the apex $1.5-2\mu$ in width. At their proximal end they are $5-13\mu$ wide, with much thinner walls and wider lumen. The thickening of the walls is thus attenuating from the apex towards the base

of these hyphae (Text-fig. 1 pa; Pl. XI, fig. 3; Pl. XII, figs. 4 a, 5). Cotton Blue stains the lumen blue, the walls greenish; improved Leischmann's stain stains the lumen pinkish and the walls a strong green.

5. PLECTENCHYMATIC SYSTEM

Constitutes the inward continuation of the palisade system. In the initial stage the hyphae are multiseptate, straight, longitudinal, hyaline, thin-walled, $3.5-4.5\mu$ wide, and $4.5-10\mu$ long. In the mature stage they constitute a paraplectenchymatic tissue with hyaline, polygonal cells measuring $3-4.5\mu$ in diameter (Text-fig. 1 B; Pl. VII, figs. 4 b, 5). Stained weakly or not at all by Cotton Blue, pinkish by improved Leischmann's stain.

6. MYCELIAL, HYPHAE

Occur in the substrate and throughout the flesh of the fruit-body and in the tubes, but not in the crust. Branched profusely, aseptate, hyaline, sometimes slightly yellowish, with thickened walls. Apparently occur in a narrower form measuring $1-2\mu$, and a broader form measuring $2.5-3\mu$ across (Pl. XIV, fig. 13). Lumen stained weakly bluish with Cotton Blue.

THE STRUCTURE OF THE FRUIT-BODY

The fruit-body of *Ganoderma lucidum* appears in the shape of either a monopodial carpophore or a hemispherical bracket attached to the tree by a rudimentary stalk (Pl. XI, figs. 1, 2).

Both these types are characterized by the cup-shaped growing zones of which they are composed. These in radial section appear as arcs. Each growing zone comprises a light and a dark arc-shaped semicircular belt which, in the case of the hemispherical bracket, extends from the upper to the lower surface of the fruit-body, or, if the fruit-body develops monopodially, from one side of the stem or pileus to the opposite side (Pl. XI, figs. 1, 2; Pl. XIII, fig. 8).

The dark belts mentioned above measure $300-500\mu$, the light belts $1000-2000\mu$ in width. In each dark belt three distinct portions may be observed under the microscope to differ by their shade of colour: A lighter central portion is limited both proximally as well as distally by darker portions (Text-fig. 1 D; Pl. XIII, fig. 8).

Of the latter the distal one owes its dark colour to the swelling of hyphal ends the walls of which thicken and turn dark brown (Text-fig. 1 ap; Pl. XIII, fig. 9). The proximal portion on the other hand appears dark in colour as there the hyphae give rise at about right angles to short and stout branches which link across and reinforce the tissue. (Text-fig. 1 bd; Pl. XIII, fig. 10). The central portion of the dark belt, though lighter than the portions just described, is still darker than the light belt. Macroscopically the whole of the dark belt appears uniformly dark.

The transition from the dark into the light belts is made by apical growth from these dark swollen hyphae. The newly formed hyphae, arising singly, in pairs, or in groups of three, are always less densely arranged than their mother hyphae with the swollen ends (Text-fig. 1 C; Pl. XIII, figs. 8, 9). The hyphae of the light belt exhibit a more uniformly longitudinal direction of growth, although their slender branches also intertwine to some extent (Text-fig. 1 E; Pl. XIII, fig. 8; Pl. XIV, fig. 12).

Branching and interweaving becomes more pronounced, as the zones or ends of zones approach the upper and lower surfaces of the fruit-body, i. e. the crust, tubes or margin, so that in the outmost two, three, or even more zones the hyphae branch profusely and are interwoven closely, representing a binding system (Text-fig. 1 B, C; Pl. XI, fig. 3). The marginal and crust regions are lighter in colour and exhibit less pronounced zonation.

Similarly fruit-bodies sometimes occur, especially in the form of dorsiventrally compressed brackets, in which zonation is less marked. In their case the kind of growth described above to be typical only of the outmost zones of normal fruit-bodies, occurs throughout the majority of their zones. The hyphae in all, and especially in the darker belts are then found to have branched profusely and to intertwine. Hyphal ends in the dark belts are also lighter in colour and less swollen than in the normal types, and the hyphae they produce are still somewhat thinner.

The crust is covered by a laccate cuticle, resinous in character, which generally dissolves if sections are mounted in lactophenol, but which remains unaffected if they are mounted in cold water or glycerine. The layer below this cuticle consists of hyphae growing

perpendicular to the outer surface, which are swollen, maintain an even level and have assumed the form of palisades described above (Text-fig. 1 A; Pl. XI, fig. 3; Pl. XII, figs. 4, 5).

Below the palisades we notice, as the next layer of the crust, a para-plectenchymatic tissue composed of polygonal cells with thin and hyaline walls (Textfig. 1 B; Pl. XI, fig. 3 b; Pl. XII, figs. 4 b, 5).

The dissepiments of the tubes are composed of skeletal or mediate hyphae which are longitudinal, flexuous, kinked, branching, and intertwining. These hyphae measure $1.5-5\mu$ (majority $2.5-3.5\mu$) in width. In young dissepiments the apices, and sometimes larger portions, of these hyphae are still plasmatic and readily stain with Cotton Blue or improved Leischmann's stain. The dissepiments measure $2-10$ mm in length, and $40-100\mu$ (majority $50-80\mu$) in width. The tubes measure $150-300\mu$ (majority $200-250\mu$) in diameter (Pl. XIV, fig. 11).

The hymenium covers the dissepiments down to the flange of their mouth. The dissepiments consist of a central column of skeletal hyphae covered by an outer layer of generative hyphae. The latter in their turn are covered by a layer of subhymenial cells from which the hymenium arises. The subhymenium and hymenium stain blue with Cotton Blue and pink with improved Leischmann's stain.

THE DEVELOPMENT OF THE FRUIT-BODY

In describing the development of the fruit-body through all its stages on the basis of mere anatomical examinations and without the support of experimental evidence, some hypothetical considerations are of course unavoidable. Nevertheless such an attempt may be useful not only for the anatomical understanding of the structure of the fruit-body, but also because it indicates on what lines future experimental studies may proceed.

The following stages may be distinguished in the development of the fruit-body, and will each be treated separately:

I. THE INCEPTION

On examination of that part of the woody substrate which bears the fruit-body, we find a skein of mycelial hyphae which project into the fruit-body and support it. These hyphae may therefore

be imagined to represent the inception stage of the primordium. The skeletal hyphae of the first proximal zone resemble the broad and thick-walled type of mycelial hypha found in the wood vessels of the host; the hyphae in this zone to some extent retain their plasmatic character and stain bluish with Cotton Blue while skeletal hyphae of the more distal growing zones do not stain thus.

CORNER (12) at length discussed the factors inducing the development of the fruit-body. Factors such as the exhaustion or accumulation of food supplies, light, and oxygen, are mentioned as inducing hyphae to grow out from the wood of the substrate to form a fruit-body. In our case of *Ganoderma lucidum* which mostly attacks trees previously weakened by adverse growing conditions, exhaustion of food rather than its accumulation would at first appear the more likely stimulant. On the other hand, weak trees are known to ripen their fruits earlier and this may indicate a higher concentration of solutes in the tree.

As will be shown later, the brighter and larger belts of the zones in the fruit-body are considered to form during day-time, while the darker and smaller belts form at night. If this is true—as it would appear to us to be—it supports the view that light and oxygen, which are more readily available to the fruit-body during the day, are factors essential for its unhampered growth.

2. THE FRUIT-BODY

The primordium formed by the hyphae emerging from the substrate appears as a small bright yellow cushion which is composed of intertwining hyphae. But the periodicity of growth soon finds its expression in the formation of zones consisting, as described above, of a light and dark belt each. After two or three zones have formed all the hyphae—with the exception of those near the margin and the upper and lower surface of the fruit-body—become fibrillar in character, and the growing zones become increasingly marked. From now onwards it is characteristic of the development of the fruit-body that growth is intermittent, and that each newly arising zone forms an arc concentric with and slightly longer than the preceding zones. Thus the growing margin is enlarged by the progressive addition of new zones.

Growing in a radial direction the hyphae diverge from each other and gaps would form between them unless this was prevented by the above-mentioned terminal branching of each swollen hyphal end in the dark belts into a number of thinner hyphae. The extent of this branching determines the thickness and the centrifugal and tangential development of the cup-shaped layer formed by the succeeding zone: if the majority of swollen hyphal ends* of one zone give rise only to one or two hyphae each, then the new zone formed by the latter will but little exceed the preceding zone in its thickness, length, and width. If on the other hand most of the swollen dark hyphal ends produce three or more hyphae each, then the zone formed in this way will extend well beyond the preceding zone in all directions.

Skeletal hyphae in all the growing zones are fibrillar in structure, except in the outermost zones adjacent to the margin and the upper and lower surface of the fruit-body, where they intertwine in the manner described above. These intertwining hyphae, especially at the upper surface and the margin, remain more or less plasmatic and stain bluish with Cotton Blue. The plasmatic nature of these zones may be explained by the fact that (1) they represent the youngest part of the fruit-body which has as yet undergone no differentiation, and (2) they are in more immediate contact with the oxygen of the surrounding atmosphere than the skeletal hyphae in the central portion of the fruit-body.

The further growth of the fruit-body proceeds by the formation of concentric, more or less semicircular zones centred on a common imaginary axis which runs perpendicular to the substrate. If the latter is horizontal then—the zones being added about a vertical axis—the fruit-body assumes an upright form (Pl. XI, fig. 1). If, however, the substrate is perpendicular to the ground, then the fruit-body, with zones continually added to it about a horizontal axis, assumes the form of a bracket (Pl. XI, fig. 2). In the former case the growing margin appears positively phototropic, while in the latter case it appears diageotropic.

In the upright type of fruit-body differentiation of the stalk and pileus seem to proceed as follows: The growing zones first formed are of more or less equal size of arc, younger zones attaining

the same size as the zones from which they arose. After a number of such equal zones has been produced in succession they together form the stalk. This stage being reached, the stimulus for the pileus formation now becomes effective. Successive zones progressively add to the length of their arc. This, as mentioned above, is due to increased apical ramification of the hyphae of the dark belts. Eventually the central portion of the fruit-body ceases growth, while the marginal portion grows out into a circular horizontal limb. Thus, instead of assuming a semispherical shape, the upper part of the fruit-body is flattened and growth is restricted to the peripheral limbs (Pl. XI, fig. 1). As in this way only the peripheral portion of each new zone continues to grow, a change in the growth of the fruit-body as a whole from a vertical to a horizontal direction is brought about without involving a deviation of the direction of growth of individual hyphae, as described by CORNER (12) in the pileus formation of *Polystictus xanthopus*.

The causes underlying the cessation of growth in the central portion of the fruit-body can only be guessed. We suggest that exhaustion of the available food-supply may be the reason. It is in the central portion of the upper surface that the hyphae first lose their plasmatic character, while in the peripheral portion of the fruit-body they remain more or less plasmatic much longer, and stain bluish with Cotton Blue.

The bracket-shaped type of fruit-body is of necessity formed wherever the primordium emerges from a perpendicular substrate. In this case the bracket is the only shape permitting the tubes to grow in that positively geotropic direction in which they are found to grow in all types of fruit-bodies, and which seems to be essential for the liberation of spores.

The initial growth of the bracket may consist in the formation of a stalk about 1 cm in length which abruptly or gradually passes into a hemispherical bracket. Alternatively a hemispherical growth may arise immediately on the substrate (Pl. XI, fig. 2). In the latter case the underside of the fruit-body sometimes extends downwards for a little way at its proximal end, and thus forms a rudimentary stalk adpressed to the substrate. The tissue of this stalk is formed by the separate growth of short successive zones around

the vertical axis of the stalk. In both these bracket-shaped types, just as in the upright type, the chief semicircular growing zones centre about an axis perpendicular to the surface of the substrate. Bracket-shaped fruit-bodies are usually broader at their base and taper towards their distal end. This gradual decrease in width may perhaps be explained by a corresponding decrease of the food supply available, those parts of the bracket which are distant from the substrate being not as well provided with food as the more proximal parts.

Dorsiventrally compressed brackets which, as mentioned above, are met with occasionally, are uniformly thick all along. Brackets of this shape also exhibit other deviations from the types above described: their zonation is less pronounced and their skeletal hyphae lose the usual fibrillar structure and are more or less interwoven. The hyphae of their central portion also stain more or less bluish with Cotton Blue. In all these features they resemble the type of growth limited in normal fruit-bodies to the outmost zones only, and this resemblance appears to suggest that compressed brackets form under conditions which in normal fruit-bodies only obtain near the margin. As stated above the hyphae in the outmost zones of normal fruit-bodies remain more or less plasmatic. This was above explained as due to their more immediate connection with the oxygen of the atmosphere; in compressed brackets, then, where the flesh is very narrow, all hyphae may be imagined to be in more direct contact with oxygen.

3. THE CRUST

The crust begins to form as soon as a few growing zones have developed in the primordium. Its yellow surface turns brown and laccate, but not uniformly so, so that yellow undarkened patches may be noticed even on mature fruit-bodies. In upright as well as in bracket-shaped fruit-bodies the crust extends well over the stalk. It constitutes a protective layer for the flesh of the fruit-body. As set out below, the crust may in certain cases also extend to the lower side of the fruit-body, especially when the latter has been pierced by a splinter of wood. In that case the crust even extends over the inside of the wound i. e. right into the flesh of the fruit-body.

Generative hyphae may first be found in those outmost two or

three zones where mediate and plasmatic hyphae usually occur. They differ from plasmatic hyphae by being septate and staining weakly or not at all with Cotton Blue. Their origin is still a matter of doubt. They might be imagined to arise by branching from the initial stages of the skeletal system and to disappear as the skeletal stroma matures. But it appears to us far more plausible to assume that the generative hyphae represent the distal ends of hyphae which directly originate in the mycelial hyphae of the substrate and which are independent of the repeated zonal ramifications exhibited by the skeletal system. Occurring always together with plasmatic hyphae at the growing margin, the generative hyphae may be thought to grow intermingled with, but independent of, the skeletal stroma. But in view of the fact that in mature portions of the fruit-body we have so far been unable to trace them among the old skeletal hyphae, we would have to conclude that their proximal portions degenerate and disappear in time. We cannot, however, preclude the possibility that they ultimately form hyphae of a skeletal type in addition to those formed by the skeletal system.

Generative hyphae grow faster than the plasmatic and mediate hyphae forming the outmost zones, and always outgrow them. While at their proximal parts these generative hyphae are distributed sparingly among the hyphae of the skeletal system, at their distal ends they approach each other, and become flattened and profusely septate so as to form a plectenchymatic tissue. After some time the ends of these hyphae elongate and form broad palisade-like terminal portions which in their young stage are characterized by their rich plasmatic contents and their strong response to Cotton Blue and improved Leischmann's stain. Their wall then thickens, especially at the apex but attenuating proximally so that the basal portion is only slightly thickened. Some time later only their narrowed lumen continues to stain blue with Cotton Blue or pink with improved Leischmann's stain, while their thickened walls stain green with the latter (Text-fig. 1 A, B; Pl. XI, fig. 3 a, b; Pl. XII, fig. 5).

Simultaneously, the proximal part of the plectenchymatic hyphae often gives rise to small lateral protuberances which protrude into neighbouring hyphae, so that the tissue becomes more and more compact and appears para-plectenchymatic (Pl. XII, figs. 4 b, 5).

As previously mentioned, the skeletal hyphae, where they approach the crust with their plasmatic terminal portions, cease to grow straight and start to branch strongly and to form a binding system (Text-fig. 1 C; Pl. XI, fig. 3 c). But this branching is less pronounced where the ends of the zonal arcs touch the crust proper.

4. THE TUBES

The tubes, as mentioned above, grow at the underside of the fruit-body and are always positively geotropic. Their growth is frequently arrested before they have commenced to function. In that case the crust may grow from the upper surface downwards around the margin until it completely covers the abortive tubes.

The zonate layers with their bent and convex ends terminate on the lower surface of the fruit-body, where the tubes arise, in the same way as on the upper surface where the crust forms. The hyphae approaching the lower surface, however, do not run straight because they ramify near the margin of the lower surface, interweave and—much as they do below the crust—form a binding system. Eventually the ends of these hyphae composing the binding tissue arrive at the lower surface of the fruit-body where the tubes are to be formed (Pl. XIV, fig. 11).

The formation of the tubes commences on the lower side of a white, finely velutinate rim, 1—4 mm wide, which in the case of compressed fruit-bodies may be brown and laccate. This zone, according to CORNER (13), is called the pore field, because it is here that the lines of force which demarcate the pores, come into play. Here the pores appear in their outlines as angular, roundish areas of restricted growth, girt by excrecent ridges. These ridges grow downwards until they assume the form of dissepiments.

If this general explanation is correct, in the case of *Ganoderma lucidum*, too, the ridges are formed by the ends of hyphae which are directed downwards by the supposed lines of force which direct them towards gravity. The tips of the extruding hyphae emerging from the interwoven layer need not even alter their direction but simply continue to grow in a straight line, more or less perpendicular to the lower margin. When they begin to grow into ridges the hyphae are plasmatic, being the extension of mediate and skeletal hy-

phae, and are stained blue with Cotton Blue and reddish with improved Leischmann's stain. After some time they are transformed into mediate hyphae, i. e. their walls thicken and they become yellow in colour; finally their proximal parts are turned into skeletal hyphae.

Their tips remain plasmatic for a long time and continue to stain blue with Cotton Blue and pinkish with improved Leischmann's stain. The hyphae of the dissepiment branch, interweave, and form a reticulate texture reinforcing the dissepiment. In the course of time these hyphae turn brown and become skeletal.

Generative hyphae are certainly intermingled with the plasmatic hyphae which give rise to the dissepiment. They appear on the outside of the latter as a thin layer, 1—4 hyphae thick. These hyphae remain hyaline, are multiseptate, 1.5μ — 3μ wide, and continue to stain blue with Cotton Blue and pinkish with improved Leischmann's stain. They produce the subhymenium and hymenium.

INTERRELATIONS OF THE HYPHAL SYSTEMS

Two fundamental hyphal systems are chiefly responsible for the formation of the fruit-body of *Ganoderma lucidum*: the generative system and the skeletal system which comprises three successive stages, the plasmatic, mediate, and skeletal hyphae. According to our observations each of these systems has a distinct function of its own in the formation of the fruit-body. The skeletal system has to form the somatic bulk of the fruit-body consisting of skeletal hyphae which undergo no further changes. The generative system, on the other hand, serves for the formation of the reproductive apparatus and the crust, and for this purpose its hyphae have to undergo considerable differentiation and transformation.

In view of the fact that these two systems of hyphae serve so clearly distinct histogenetic purposes, a direct bodily transformation of one system into the other can hardly be expected to be the rule. We have in fact so far been unable to observe any such direct transformation of generative into mediate and skeletal hyphae. The thin-walled colourless hyphae in which mediate or skeletal hyphae terminate, were always found to be plasmatic and not generative hyphae i. e. to represent the initial stage of the skeletal system which later develops into mediate and then into skeletal hyphae. Plasmatic hyphae

resemble generative hyphae by their thin walls, but differ from them by the complete absence of septae and by staining strongly with Cotton Blue.

It is thus evident that the origin of both these hyphal systems is not easily explained. The examination of the proximal zonate layer adjacent to the substrate did not so far yield any evidence on this point. The above expressed assumption that the two systems might have a common origin in the mycelium emerging from the substrate appears to us the most likely. But we were unable to trace where differentiation for the distinct function of each system takes place.

ZONATION

As stated above the marginal growth of the fruit-body of *Ganoderma lucidum* is intermittent and proceeds in a series of small bursts of growth. This phenomenon has been reported by CORNER (13) for many species of *Fomes*. FALCK (15) is the only author who has described this type of growth in detail for the fruit-bodies of *Merulius domesticus*. He distinguished between what he called natural and artificial zones formed in this manner. In the case of those fruit-bodies of *Merulius* which adhere to the substrate with the whole of their lower surface, he proved adequacy of the food supply to be the factor governing the formation of zones. If the food supply is ample, then the hyphae, after first growing straight and in radial direction, begin to branch. The areas of radial growth and of branching are then marked off against one another as distinct zones. FALCK further supported his theories of zonation by experiments and observations on zone-formation in mycelia grown in Petri dishes.

In the case of the bracket-shaped, free-growing fruit-bodies of *Merulius* FALCK attempted to explain zonation as due to the action of the force of gravity which, in his opinion, exerts an influence comparable to that exerted by the food supply factor. But while the predominance of the latter furnishes a satisfactory explanation of zonation in the fruit-bodies adhering fully to the substrate, yet the gravitational explanation given for the free-growing fruit-bodies does not convince us and must be regarded as an unproven hypothesis.

However, FALCK's theory of the formation of artificial zones where growth has been checked (Hemmungszonen) seems to us to

afford an explanation of natural zonation also in the case of *Fomes* and *Ganoderma*.

FALCK (15, p. 83) has proved experimentally that the discoloration of the hyaline mycelium may be brought about by strong light, high temperatures, and high concentrations of food supplies. More recently CHODAT (11) and MAURIZIO and STAUB (23) have demonstrated by experiments that in culture blackening of the mycelium may be induced by high concentrations of sugars, especially of dextrose. Old mycelia are known to swell and thicken at times when they suffer from the lack or excess of certain nutritional ingredients. BURRI and STAUB (10) artificially induced the thickening of hyphal walls by depriving the mycelium of the oxygen it requires. There is thus ample evidence that external factors may check growth and induce thickening and darkening of hyphae.

In view of the fact that in zonal growth the checks received are periodic and appear at short intervals we have to search for a factor exhibiting a similar periodicity, and there the alternation of day and night immediately offers itself as by far the most likely. CORNER (13) indeed suggests a correlation between the formation of zones and the alternation of day and night in *Fomes levigatus*. He supports his hypothesis by very conclusive evidence, as he found the width of a zone to correspond to the daily increment of marginal growth.

We thus agree with CORNER that zonation in the case of *Ganoderma lucidum* as well may be correlated with the periodical influence of day and night and that dark zones form at night. But we are unable to accept the reasons he furnishes in explanation of this phenomenon. His argument is that the greater abundance and closer spacing of hyphae in the dark zones may be explained as due to increased nocturnal humidity, whereas the light zones may form during the day when humidity is low and hyphae therefore grow less densely and free from one another. This explanation does not in our case fit the facts. The swollen hyphal ends of each dark belt, as indicated above, ramify terminally into two or three new hyphae, so that the newly formed light belt actually contains more hyphal growth than the dark belt which it arose from. We can therefore not agree that hyphal growth is more abundant in the dark than in the light belts.

To us the causes for the dark appearance of the dark belts appear to be as follows: (1) The swollen hyphal ends approach each other, and thus make the tissue appear denser and therefore darker; (2) the hyphae in the dark belts are actually somewhat darker in colour than those in the light belts; (3) the dark appearance is further accentuated by the manner in which the hyphae of the dark belts branch. This is characterized by the formation of binding branches approximately equal in width to the mother-hyphae at about right angles to the latter. In the light belts branching is altogether less profuse and the branches, radiating in all directions, are much narrower and lighter than the mother-hyphae (Text-fig. 1 D, E; Pl. XIII, figs. 8, 9, 10; Pl. XIV, fig. 12).

On the other hand, what makes the hyphae of the light belts appear free and more liberally spaced, is that (1) the hyphae in these belts are so slender that even all those arising from a common dark apex, if taken together, mostly do not cover the entire surface of this apex so that empty spaces are left between them; (2) as the fruit-body of *Ganoderma* grows by the successive addition of arc-shaped zones, each zone is bound to be somewhat wider than the preceding zone. This naturally results in wider spacing of the hyphae (Text-fig. 1 D, E; Pl. XIII, figs. 8, 9; Pl. XIV, fig. 12).

We therefore arrive at the conclusion that the light belts, although actually richer in hyphal growth, appear light owing to the wider spacing and lighter colour of their hyphae. It follows that in our case, in contrast to the case studied by CORNER, the growth made at night—so far from being richer than that made during the day—represents growth checked by unfavourable conditions.

The question now arises as to the nature of the external factors which check growth at night and thus produce the dark belts. In our opinion the factors responsible appear to be:

I. THE ACCUMULATION OF CARBON DIOXIDE IN THE AIR AND THE TREE

High concentrations of carbon dioxide have long been known to hamper the development of certain fungi. FALCK first observed this in his work on the timber rotting fungus *Merulius*. BROWN (9) demonstrated in 1922 that 20% or even 10% of carbon dioxide in the air have a strongly inhibitive effect on the development of

Botrytis cinerea and of *Sclerotinia cinerea* grown on apples. GASSNER and STRAIB (17) found that concentrations of carbon dioxide of about 3—4.5% inhibited the infection of cereals by rusts. BAVENDAMM (1) in 1928 published a comprehensive investigation into the influence of carbon dioxide on the development of 32 wood-rotting fungi, the majority of which belonged to the *Polyporaceae*. He found that 19% of carbon dioxide in the air are very injurious to the growth of these fungi. But it was only by accident that his experiment was interrupted at this concentration, and he believed that even lower concentrations would also inhibit the growth of these fungi. He writes on p. 528 "Da aber 19% durchaus noch nicht die Grenze der Hemmung darstellen, sondern auch noch bei geringeren Kohlensäuremengen deutliche Hemmungserscheinungen zu erwarten sind, duerfte die Zahl eher zu hoch als zu niedrig angesetzt sein".

At night carbon dioxide is known to accumulate to higher concentrations both in the air and in the tree than during the day. This is due to the lack of assimilation, decreased transpiration, and increased respiration of plants and soil micro-organisms. LUNDEGARDH (22) found that in a field of beet-roots the carbon dioxide concentration in the soil at 6 p. m. was higher by 10% than at noon. Still higher concentrations may be imagined to prevail at night.

An excess of carbon dioxide in the air may act on the fungus either directly by its effect on the fruit-body or indirectly by its effect on the tree which may then be imparted to the mycelium. According to BOEHM and DOUGLAS, as quoted by BAVENDAMM (1), very high concentrations of as much as 54% carbon dioxide may occur within trees and are certain to rise even higher at night.

It should further be pointed out that the low temperatures prevailing at night accentuate the inhibitory effect which an excess of carbon dioxide exerts on the growth of the fungus.

2. HIGH CONCENTRATION OF SUGARS

We have mentioned above the investigations of FALCK (15), CHODAT (11), and MAURIZIO and STAUB (23) which indicate that a high concentration of sugars, and especially of dextrose, may have an inhibiting effect on mycelial growth. This condition may obtain at night. The starch formed in the leaves by assimilation during the

day, is at night hydrolyzed to sugar which descends the stem in solution. This has first been demonstrated in 1888 by JULIUS SACHS (28) by means of his iodine test. More recently HUBER et al. (19) succeeded in proving by thermo-electrical measurements that the concentration of sap in the stem at 6 p. m. is more than double its concentration at noon. At night the mycelium may therefore be imagined to experience an influx of highly concentrated sugar solutes, consisting, according to BENECKE and JOST (3, p. 280), mainly of dextrose, which seems to have an inhibitive effect on the hyphal growth of the fungus. This effect in our case finds its expression (a) in the blackening of the hyphae, as observed in their experiments by CHODAT (11) and by MAURIZIO and STAUB (23); (b) in the swelling of hyphal apices at the distal end of each dark belt. When the substrate mycelium is flooded with concentrated sugar solutions, growth is upset because on the one hand the process of hyphal elongation is checked while on the other hand food continues to be taken up incessantly. The hyphal apices therefore have to swell in order to accommodate the excess of food. Many cases are known of green plants in which the stem swells if growth is checked while food continues to be supplied.

3. LACK OF OXYGEN

With the increase of carbon dioxide in the air and especially in the tree a corresponding decrease of oxygen occurs at night, and may this have an inhibiting effect on hyphal growth. The importance this may have an inhibiting effect also been mentioned by CORNER (12) who goes so far as to say that it is "a large amount of oxygen or a small amount of carbon dioxide in the atmosphere which lead the hyphae into the open". The role of oxygen in the growth of fungi has also been stressed by BAXTER (2), BOSE (5), LONG and HARSCH (21), and others as mentioned by BAVENDAMM (1).

Further evidence that the dark belt of each zone is formed at night while the light belt is formed during the day may be seen in the fact that the former only attains about half the size of the latter. This agrees with the relative duration of the night and day time growing periods, as in summer, when the fungus develops, the nights are much shorter than the days.

The assumption that the dark belt of each zone with its swell-

len hyphal ends forms at night, may further explain why the width of the hyphae arising from these swollen ends is always much less than that of their mother-hyphae (Text-fig. 1 D; Pl. XIII, fig. 9). The humidity prevailing at night accustoms the growing hyphae to moist conditions. Thus, when humidity decreases in the morning, the hyphae for some time suffer from drought and their width becomes much reduced. FALCK (15) has proved experimentally that such a reduction of hyphal width in fact occurs where hyphae are transferred from humid to dry conditions.

In view of all the above considerations it must be admitted that there is strong evidence indicating that the dark belts form at night while the light belts form during the day.

WHITE STRANDS

A conspicuous feature, common to all specimens of fruit-bodies of *Ganoderma lucidum* we examined, was the occurrence of white strands permeating both the monopodial and the bracket-shaped types. These strands originate at the point where the fruit-body is attached to the substrate and while branching permeate the entire fruit-body to the outmost zones below crust, margin, and tubes (Pl. XI, figs. 1, 2). On examination of the strands we found them generally to contain mycelial hyphae, such as occur in the tissues of the host, which seem to parasitize on their own fruit-body. These hyphae had apparently undergone none of the physiological changes which the other hyphae had passed before taking part in the formation of the fruit-body, and retained their parasitic character even at the expense of their brother hyphae. These mycelial hyphae cause the cytolysis of all that tissue of the fruit-body which they pass through. Under their influence the hyphae of the fruit-body first lose their brown colour and become pale and then white, while later they dissolve altogether and cavities arise in their place (Pl. XIV, fig. 13). As the mycelial hyphae grow longitudinally across the fruit-body the cavities are also longitudinal in shape, and the white strands are nothing but discoloured strips of tissue in which longitudinal cavities have arisen by the cytolytic action of the mycelium. Mycelial hyphae were found to penetrate as far as the tubes and to block them; in that case the crust grows downwards around the margin and covers

the abortive tubes. The mycelium has never been found to occur in the zone immediately below the crust or in the crust itself.

The examination of microscopic sections of the white strands revealed that internal spores frequently grow in them. These spores also form within the tubes and then line the walls of the latter together with the basidiospores. They occur most abundantly in those tubes which have been covered by the crust overgrowing the pore region and blocking the pores.

Two forms of spores are apparent, one being smooth and oblong, and the other rough and round. The smooth spores are provided with two appendices on one or on both their ends. They measure $8.5\text{--}17\mu$ (majority 12.5μ) in length and $7\text{--}8.5\mu$ in width. Their membrane is 1.5μ thick. The round spores are covered by a $2.5\text{--}3\mu$ thick exosporic and a smooth, thin endosporic wall, and have a total diameter of $12\text{--}22.5\mu$ (Pl. XIV, fig. 13). Both forms of spores stain blue with Cotton Blue and reddish with improved Leischmann's stain, except the exospore of the round form which remains brownish.

More detailed examination of these two spore forms revealed them to represent successive stages of the same spore. The spores arise along the whole length of mycelial hyphae as elongated swellings of the latter, which then split into a number of oblong fragments each bearing a young spore with appendix-like pieces of hyphae. Later they round off and lose their appendices.

This type of internal sporing was first observed by PATOUIL-LARD (25) on *Ganoderma collossum*, but no significance was attached to it at the time. HEIM and MELANCON (18) described such spores in greater detail for *Ganoderma rivulosum*, and called them Gastros-pores. BOSE (6) was the first to find them in *G. lucidum*.

DISCUSSION

In the light of the above results of our anatomical investigation of *Ganoderma lucidum* much useful information may be gained by first considering our findings in relation to earlier observations of other authors with the same fungus, and then by comparing them with the results of anatomical studies of other Polyporaceae.

One of the most characteristic anatomical features of the

fruit-body of *Ganoderma lucidum*, the palisade layer, has been observed and described by several authors (4, 8). But most of these descriptions are not at all detailed and rather meagre, and hardly convey a clear idea of how these authors imagined the transition from the palisades to the hyphae of the flesh to take place. VAN DER BIJL (29) is the only investigator who discloses his opinion on this subject by a drawing of the palisades and the adjacent hyphae. This drawing, which we reproduce in Pl. XII, fig. 6, indicates what this and probably other authors imagined to be the interrelation of these hyphae. According to this drawing VAN DER BIJL believed the palisades at their proximal ends to pass over into simple individual hyphae separated from each other by empty spaces. This description does not agree with our repeated and detailed observations, as we always found the proximal ends of the palisades to pass over into a compact plectenchymatic tissue. Observing the formation of this tissue from its very inception we found the hyphae which constitute the proximal continuation of the palisades to unite and then to divide into small cells (Text-fig. 1 B; Pl. XII, fig. 4 b). The tissue thus becomes truly paraplectenchymatic and the original hyphal elements can hardly be recognized (Pl. XII, fig. 5). We observed such plectenchyma to form in all the specimens which we studied and which were taken from various hosts. It was also present in the crust where the latter abnormally overgrew tubes which have ceased to function.

CORNER (12) considered that only those hyphae which perform a special function in the formation of the fruit-body are to be designated as special systems. Accepting the principle of his classification we distinguish five hyphal systems in *Ganoderma lucidum*. The first is the skeletal system comprising skeletal, mediate, and plasmatic hyphae, which may all be considered as developmental phases of the same system and together compose the somatic or vegetative part of the fruit-body. This system may therefore also be called the vegetative system.

The second system to be distinguished is the binding system, corresponding to the binding system described by CORNER for *Polystictus xanthopus*. This system of branched and interwoven hyphae is called by OVERHOLTS (24, p. 1706) a "hyphal complex" but we prefer CORNER's term as clearer and indicative of the physiolo-

gical functions. The difference between the binding system of *Ganoderma lucidum* and that of *Polystictus*, however, is that in the latter fungus the binding hyphae form one continuous layer; whereas in *Ganoderma lucidum* there are two distinct types of binding hyphae occurring in various parts of the fruit-body in addition to the binding hyphae below the crust and at the base of the tubes which, it would appear, may be considered as a continuous layer enclosing the fungal stroma. In any case they all have the common function of strengthening the tissues. Incidentally, CORNER (13) himself admits on p. 58 and p. 66 that in *Fomes levigatus* which resembles *Ganoderma lucidum* by its intermittent marginal growth, the interwoven hyphae near the tubes are of the nature of binding hyphae; but he does not place them into a system of their own. It may be stressed that OVERHOLTS (24, p. 1706) in agreement with us also considers the interwoven binding hyphae of *Ganoderma lucidum* as homologous with the binding system of *Polystictus*.

The third hyphal system in this classification is the generative system, the hyphae of which have the function of producing a new tissue totally different in structure from the original hyphae, viz. the crust and the hymenium.

As the fourth hyphal system we may consider the palisade tissue of the crust which serves to protect the fruit-body.

The fifth hyphal system is constituted by the plectenchyma below the palisades which serves to strengthen the fruit-body.

Adopting CORNER's terminology, the fruit-body of *Ganoderma lucidum* may therefore be characterized as pentamitic, as it is composed of five different hyphal systems.

Far more involved than the morphological distinction of these hyphal systems is the description of their mutual interrelations, i. e. the transformation, if any, of one system into another. In this respect the most important problem is that of the origin of the skeletal hyphae. Our opinion for the case of *Ganoderma lucidum* has been stated in full in a previous section of this paper, but it may be briefly summarized here for the sake of contrasting it with other opinions.

We consider the skeletal to be independant from the generative

hyphae. The physiological differentiation of the skeletal system appears to start as early as in the primordium: a number of hyphae on emerging from the substrate at once exhibit the capacity of transforming their proximal parts into skeletal hyphae while their central parts remain mediate and their distal parts plasmatic, so that three successive portions may be distinguished. The further development of the skeletal system then proceeds approximately as follows: The plasmatic portion of the hyphae gives rise to a new zone and in its turn becomes mediate and later skeletal and so forth, until marginal growth ceases. In this way the growing margin always comprises the initial phases of the skeletal system, i. e. plasmatic and mediate hyphae. These are found in the marginal region side by side with the generative hyphae from which they differ only by being aseptate. Apart from those skeletal hyphae which directly emerge from the substrate the skeletal system therefore develops solely by the successive terminal ramification of the distal plasmatic ends of skeletal hyphae. In view of the fact that the skeletal system thus possesses a method of propagation of its own, there is no need to assume that generative hyphae play any part whatsoever in the development of the skeletal system.

FALCK (15) in his monograph on *Merulius* states that the skeletal hyphae in the fruit-bodies of this fungus derive from generative hyphae (which he terms "Bildende Faeden"). He writes on p. 199: "Zwei Arten der Entstehung konnten daher verfolgt werden: das eine Mal wurde beobachtet, dass die Faser sich in allmählichem Uebergang von einer unverdickten Hyphe herleitet, die den Charakter . . . der bildenden Faeden besitzt."

CORNER (12) in his first paper on *Polystictus xanthopus* believes that the skeletal hyphae form laterals of the generative hyphae. He writes on p. 88: "There is little doubt the generative system provides the skeletal hyphae, yet not by bodily transformation of its own members, since that would imply thick-walled, septate and branched hyphae, but indirectly from laterals 1.5—2.5 μ wide, the apices of which gradually expand to 3—4 μ , while the wall begins to thicken". In his second paper dealing with *Fomes levigatus* CORNER (13) writes on p. 56: "The origin of the skeletal hyphae from the generative hyphae can be observed directly in this species . . . The

generative hyphae lose the power of septation, become rather thick-walled, and stop branching . . . Their apices then enlarge slightly and the walls thicken, and they become skeletal hyphae”.

According to these observations the generative hyphae are therefore assumed to be the fundamental elements from which the skeletal system derives. Our investigations into the interrelation of these hyphal systems in the case of *Ganoderma lucidum* do not, however, corroborate the conclusions arrived at by FAIRC and CORNER. In spite of repeated attempts we never succeeded in tracing back skeletal hyphae to generative hyphae either directly or indirectly by way of the lateral branches of the latter. On the contrary we noticed in all of the numerous sections made from various parts of the fruit-body of *Ganoderma lucidum* that skeletal and generative hyphae developed next to but quite independent from each other. Side by side growth of these two systems can be well observed only in the outmost zones of the growing margin and near the inception of the dissepiments (Text-fig. 1 B, E; Pl. XII, fig. 7). In the older growing zones only indurated skeletal hyphae are conspicuous. Generative hyphae are easily distinguished from skeletal hyphae where the latter are already in their mediate phase, i. e. yellowish, aseptate, and with slightly thickened walls, while generative hyphae are colourless, septate, and thin-walled. But the two systems are not so easily distinguished where the skeletal hyphae are still in their plasmatic stage, with walls as yet unthickened (Text-fig. 1 A, B; Pl. XII, fig. 7). Both plasmatic and generative hyphae then agree in being thin-walled, and rich in plasma, and this initial phase of skeletal hyphae reacts to Cotton Blue even more strongly than generative hyphae. The only certain criterion of distinction is then septation, as plasmatic hyphae are never, generative hyphae always, septate. In addition plasmatic hyphae tend to branch terminally in response to the periodic external influence which has above been explained to be responsible for the zonation of the fruit-body. Generative hyphae, on the other hand, do not usually ramify in this fashion, and terminal ramification may thus be regarded as characteristic of the skeletal system.

No connection between these two systems has been detected and the plasmatic phase of skeletal hyphae could be traced backwards zone by zone down to the substrate. There is therefore no

reason to assume that in *Ganoderma lucidum* skeletal hyphae are derived from generative hyphae with which they have no connection. In our opinion all the evidence supports the much more convincing explanation that the hyphae emerging from the substrate at once differentiate into a vegetative or skeletal and a reproductive or generative system. The former proceeds to build up the somatic or vegetative part of the fruit-body by prolonged intermittent growth while the latter system serves to produce the crust on the upper surface, and the margin and spore-producing organs at the lower surface of the fruit-body.

CORNER (13) dealing with *Fomes levigatus* which to some extent resembles *Ganoderma lucidum*, gives an exact and beautiful description of both systems. He writes on p. 71: "The structural dorsiventrality of the pileus in *F. levigatus* is brought about by the generative system. If no crust of tubes were developed, both upper and lower surfaces would have the same structure. In any case the skeletal stroma, formed by marginal growth, is isobilateral, and the generative hyphae, which are equally distributed throughout, give rise at each surface, just behind the margin, to similar excrescent branches. A physiological distinction then appears. The force which generates the dissepiments is limited to the lower side. . .".

If this is so, why not assume that the histological and physiological distinction appears already in the first zone of the primordium, and that the two systems proceed independently from each other to form the vegetative and reproductive parts of the fruit-body respectively? What evidence is there to lead CORNER to the conclusion that the skeletal system is derived from the generative system? The single cases in which the transformation of one kind of hypha into another type has been observed, are certainly not conclusive as evidence for the mode of formation of the bulk of the fruit-body in *Ganoderma lucidum*, nor, it would appear, in *Fomes levigatus*.

It further strikes us as remarkable that CORNER, although he assumes skeletal hyphae to arise by transformation of generative hyphae, yet admits the occurrence of both kinds of hyphae in the primordium of *Fomes levigatus*. He says on p. 59 (13): "... the primordium first appears as a small fleck on the wood and rapidly

enlarges into a hemispherical body. It is . . . composed of skeletal and generative hyphae which grow out in all directions". If, then, the differentiation of the two systems is noticeable even in the primordium; CORNER's assumption that one system develops from the other appears to us far less convincing than the assumption that each system arises independently from the very beginning of the growth of the fruit-body. In the case of *Ganoderma lucidum* we seem to have been able to confirm this view by actual observation and the skeletal system there certainly appears to constitute a self-contained unit.

It is interesting to note that CORNER in the passage last quoted clearly speaks of the two hyphal systems as growing side by side. If, then, these systems grow alongside each other from the time when the primordium forms until the fruit-body reaches maturity, it appears more consistent to attribute to each of them a special function such as we have outlined above.

The critical study of the papers by FALCK (15) and CORNER (13) reveals that some of their findings are capable of interpretations widely differing from those suggested by the authors. Thus FALCK, in studying the zonated fruit-bodies of *Merulius* in order to investigate the hyphal nature of the different zones, on p. 46 arrived at the following results: The two outermost zones of the growing margin, extending until 2 mm below the margin are composed of colourless, plasmatic hyphae of the type of "Haupt- und Stammhyphen des Oberflaechenmycels". In the next 3—5 zones extending inwards until 10 mm below the margin the hyphae show all transitory stages from plasmatic to typically skeletal hyphae. The 7th zone and the zones still further inside are all typically skeletal. It follows from FALCK's description that the distal zones of the fruit-body contain a certain type of colourless hyphae which cannot be identical with generative hyphae (Bildende Faeden), as of the latter he says on p. 39: "... doch ist es immer aeusserst schwierig sie in den Hyphensystemen zu finden und ihren Verlauf zu verfolgen". The colourless hyphae of the outmost growing zones therefore clearly differ from the generative hyphae to which FALCK ascribes the origin of skeletal hyphae. It is thus difficult to understand how FALCK imagined the proximal ends of skeletal hyphae to belong to the generative system, while their distal ends do not belong to the same system. The development of the zonate fruit-body of *Merulius* appears in fact to follow the same

lines as that of *Ganoderma lucidum*; the original hyphae, from which the skeletal hyphae have arisen, then belong to the same system as the hyphae at the distal portion of the growing margin which are simply what we call the young plasmatic stages of the skeletal system. The inconsistency of FALCK'S description seems to us to be due to the close resemblance between generative hyphae and plasmatic hyphae which in *Merulius* appear to differ in their physiological properties only.

CORNER (13) in his study of *Fomes levigatus* similarly seems not to distinguish between these two kinds of hyphae. In his very interesting and detailed description of the development of the tubes he says on p. 62: "The compactness of the pore field . . . is due to the great amount of branching among the generative hyphae in the lower layer of the flesh . . ., it (the flesh) is already dark brown like the mature pores, because many of these laterals have begun to develop into the skeletal hyphae of the dissepiments and to acquire the thick, dark yellow-brown walls". It must appear very doubtful whether these colourless hyphae which later become skeletal were in fact all generative, and not rather the young stages of the skeletal i. e. the plasmatic hyphae. In our case of *Ganoderma lucidum*, as described above, we found a similar intertwining layer of hyphae with the appearance of a binding layer. But we could always more or less trace this layer back to the skeletal system. Most of the colourless hyphae taking part in the formation of dissepiments were established to be the distal plasmatic portions of skeletal hyphae, and we venture to suggest that the bulk of the colourless hyphae observed by CORNER in the pore field of *F. levigatus* might similarly be interpreted as plasmatic hyphae. Intermingling with these hyphae of the skeletal system there are of course generative hyphae which enter the dissepiment in order to form the hymenium. But these only constitute a small part of the colourless hyphae, and, before all, always remain colourless.

CORNER (13) himself appears to have noticed some differences between these two types of colourless hyphae occurring in the tube region. On p. 64, for example, he writes: "Many of the laterals remain thinwalled but in others the walls have become more or less indurated and yellowish-brown and yet others have become narrow

skeletal hyphae". On p. 67 CORNER writes of these same hyphae: "Moreover there are irregularities in the deportment of the generative hyphae; for some of them stop growing and their walls thicken up to the apex, and then delicate, colourless processes are frequently extruded which grow on as ordinary generative hyphae and apparently contribute to the hymenium". It would appear to us that a better explanation of the whole anatomical structure of *Fomes levigatus*, would be afforded by the assumption that the first type of hypha described by CORNER as later becoming indurated, represents the initial stage of the skeletal system—the plasmatic hyphae—while his second type of delicate, colourless hypha represents the genuine or, as CORNER says, the "ordinary" generative hyphae taking part in the formation of the hymenium. In other words we consider all those hyphae which are concerned in the formation of the somatic part of the fruit-body of *Ganoderma lucidum*, and, it would appear to us, of *Fomes levigatus* and *Merulius domesticus* as well, as belonging to the vegetative or skeletal system, while the hyphae taking part in the formation of crust and hymenium belong to the generative system.

In conclusion we should like to quote once more from CORNER's paper (13) what appears to us not to be entirely consistent with his view that the newly arising narrow skeletal hyphae in the dissepiments are formed from laterals of generative hyphae. CORNER writes on p. 70: "As regards the details of the geotropic mechanism much can be learned from the manner of growth of the hyphae. From their straight course and from the fact that they form the bulk of the tissue and lead the marginal growth, it is natural to conclude that the skeletal hyphae are the sensitive elements. But whether the main generative hyphae, which grow radially in the flesh, are also geotropic cannot be decided . . . ; the possibility is precluded however from their laterals which wander about".

But it is just these non-geotropic "laterals of the generative hyphae" which CORNER considers to give rise to the geotropic skeletal hyphae of the dissepiment. It seems to us unlikely that two stages of the same system should differ so widely in their geotropic behaviour and the actual existence of this difference strongly supports our assumption that the skeletal and the generative system are entirely independent from each other.

SUMMARY

A description is given of the anatomical structure of the fruit-body of *Ganoderma lucidum*, collected in Palestine from six different hosts.

The growth of the fruit-body may be monopodial, and then positively phototropic, or bracket-shaped, when it is diageotropic.

Five distinct systems of hyphae are concerned in the construction of the fruit-body: the aseptate skeletal system which comprises a thin-walled—plasmatic, a slightly thick-walled—mediate, and lastly a thick-walled—skeletal phase of development; the septate generative system which is plasmatic and colourless; the binding system appearing in various positions in the dark and light belts of the growing zones, near the crust, and near the tubes; the palisade system covering the upper surface of the fruit-body and composed of a continuous row of broad hyphae which are very thick-walled at their distal ends; and finally the plectenchymatic system which consists of polygonal cells with hyaline walls.

The respective physiological functions of these systems are as follows: The skeletal system composes the somatic part of the fruit-body and the dissepiments; the generative system gives rise to crust and hymenium; the binding systems serve to strengthen and consolidate the texture of the fruit-body; the palisade system constitutes an external protective layer; the plectenchymatic system closely knits together and compacts the tissue of the fruit-body.

The skeletal and the generative hyphae grow essentially independent from each other. They appear to differentiate as early as in the primordium, immediately after emerging from the mycelium of the substrate.

The fruit-body develops by intermittent growth which finds its biological expression in the production of alternating light and dark arc-shaped belts constituting well-defined zones of growth. This mode of growth seems to be due to the periodic influence of day and night. At night the hyphae darken and swell at their ends, while those arising in day-time are narrower and lighter in colour. The swollen ends of the dark hyphae may ramify terminally and in this way increase the thickness and the centrifugal and tangential development of the cup-shaped zone succeeding it.

The darkening and swelling of hyphal ends to form the dark belts is held to be due to the inhibitory effect during the night of an excess of carbon dioxide and a concurrent shortage of oxygen in the air and tree, and to a simultaneous excess of sugar solutes in the stem.

Both bracket-shaped and monopodial types of fruit-bodies arise by the successive development of semicircular growing zones about an axis perpendicular to the surface of the substrate. With the former type this surface is vertical, with the latter horizontal.

The examination of white strands permeating the fruit-bodies revealed that the pale-coloured hyphae and cavities in the flesh are formed by the cytolytic action of hyphae of the substrate mycelium apparently parasitizing on the fruit-body. So-called gastrospores were found in these cavities.

The development of the fruit-body of *Ganoderma lucidum* is compared with that of *Merulius domesticus*, as described by FALCK, and that of *Fomes levigatus*, as described by CORNER. Contrary to the opinion of these authors, who believe skeletal hyphae to originate from generative hyphae, it is suggested that in *Ganoderma lucidum*, and possibly in the species they studied as well, the skeletal system is self-contained i. e. develops zone by zone from the primordium onwards, each zone forming from the plasmatic portions of the skeletal hyphae of the preceding zone. The hyphae of this system in the course of their development thus pass through plasmatic and mediate phases until finally they become skeletal.

* * *

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EXPLANATION OF PLATES

PLATE XI

- Fig. 1. Median section through monopodial, upright fruit-body growing on horizontal substrate. Arc-shaped zones, centred about an axis perpendicular to the substrate, successively increase in length until growth ceases in the centre and the lateral portions only continue to grow into the limbs of the pileus. White strands are seen in the lower portion ($\times 0.80$).
- Fig. 2. Median section through bracket-shaped fruit-body growing on vertical substrate, showing semicircular zones and tubes. Arc-shaped zones centre about an axis perpendicular to the substrate. The whitish lines in the stroma represent white strands ($\times 0.80$).
- Fig. 3. Section through outer portion of fruit-body showing, *a* palisades, *b* paraplectenchyma, *c* intertwining binding system composed of plasmatic and mediate hyphae, and *d* longitudinal skeletal system. The small black grains are precipitates of Leischmann's reagent ($\times 230$).

PLATE XII

- Fig. 4. Section through the young crust showing palisade layer *a* and plectenchyma *b* in initial stage. In the former the generative hyphae *d* approaching each other become multi-septate and form protuberances. The ends of two mediate hyphae *c* are seen on the right. Three spores have accidentally entered the left portion of the section ($\times 800$).
- Fig. 5. Section through the crust showing plectenchyma and palisade layer at a later stage. In the former the tissue has become more compact and paraplectenchymatic. Mediate hyphae, stained blue by Cotton Blue, appear at its proximal portion ($\times 700$).
- Fig. 6. Palisades and adjacent hyphae of *Ganoderma lucidum* as drawn by VAN DER BIJL (29).
- Fig. 7. Section through marginal zone showing plasmatic hyphae, stained blue by Cotton Blue, with the terminal ramifications characteristic of the skeletal system. In the back-ground septate generative hyphae (unstained) are still just discernible ($\times 700$).

PLATE XIII

- Fig. 8. Section through part of the zonal region showing a dark belt in the centre. The dark line limiting it above is constituted by dark swollen hyphal ends, the line below by binding hyphae branching at approximately right angles. Portions of the adjacent light belts are seen above and below ($\times 70$).

- Fig. 9. Section through distal black portion of a dark belt showing hyphae with dark swollen ends which ramify terminally into two or three branches ($\times 500$).
- Fig. 10. Section through proximal black portion of a dark belt showing binding hyphae branching at approximately right angles ($\times 230$).

PLATE XIV

- Fig. 11. Section through the base of the tube region showing intertwining binding hyphae. Below appear the bases of dissepiments, above the longitudinal texture of the more central portions of the fruit-body. ($\times 130$).
- Fig. 12. Section through portion of a light belt showing slender, intertwining binding hyphae ($\times 200$).
- Fig. 13. Section through a white strand stained blue by Cotton Blue. A cavity has formed by the cytolytic action of the mycelium. Note the dissolved hyphae of the fruit-body, mycelial hyphae, and gastrospores ($\times 570$).

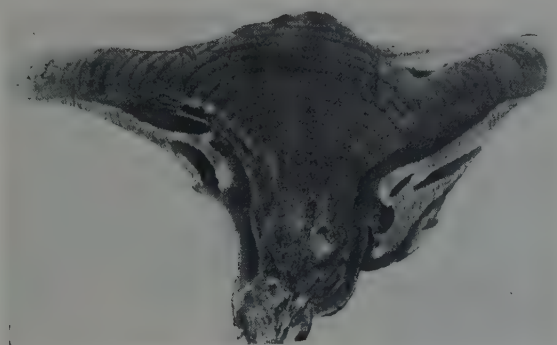


Fig. 1

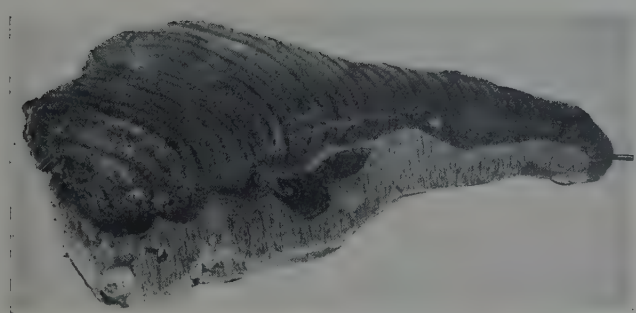


Fig. 2

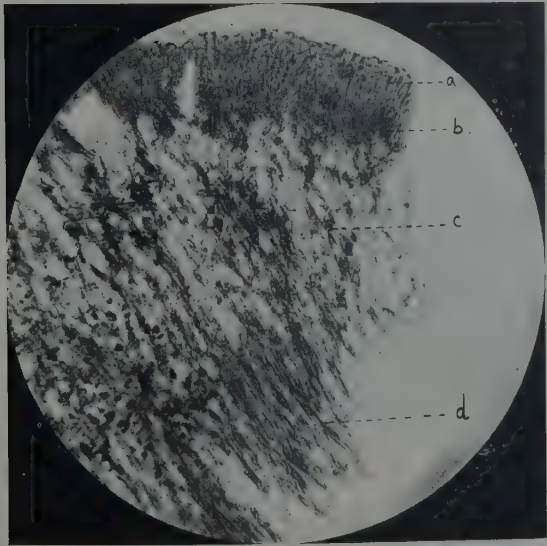


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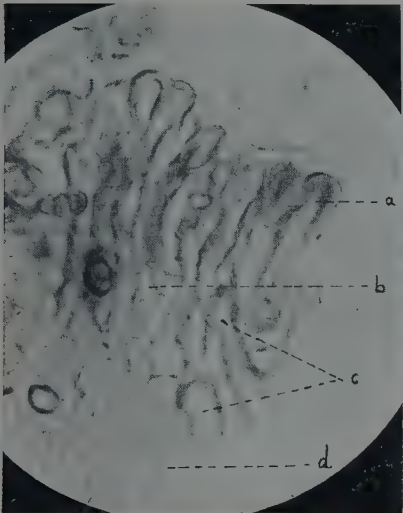


Fig. 4

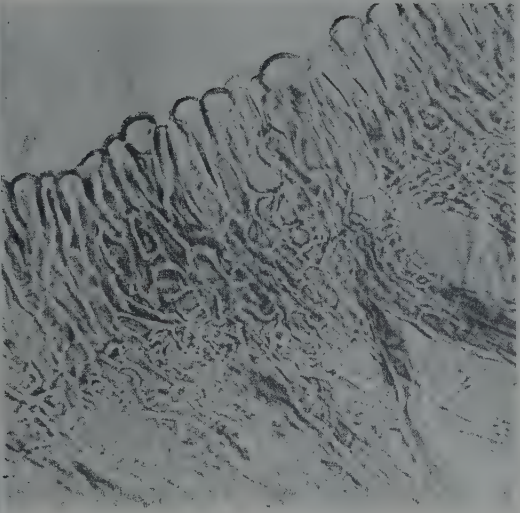


Fig. 5

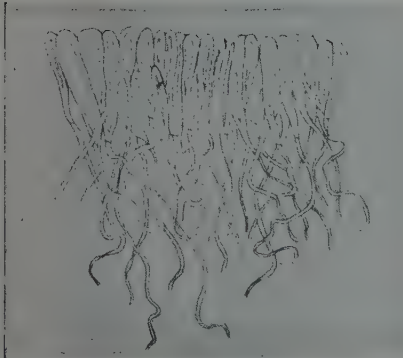


Fig. 6

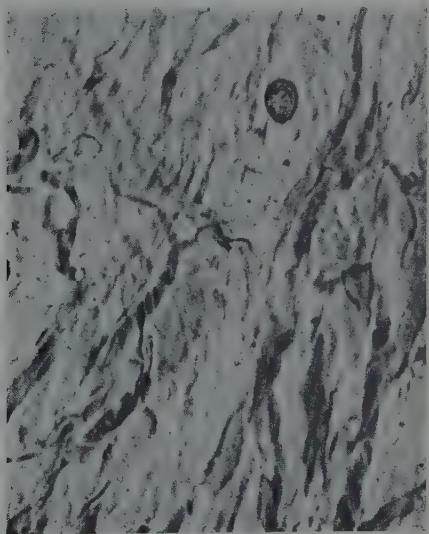


Fig. 7

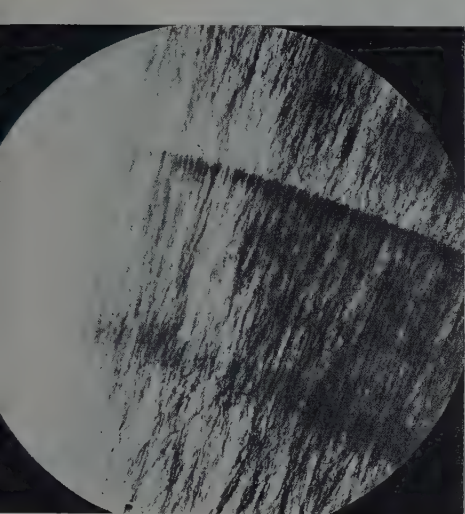


Fig. 8

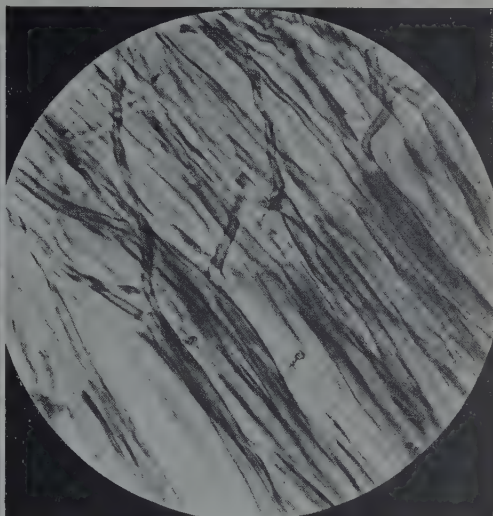


Fig. 9

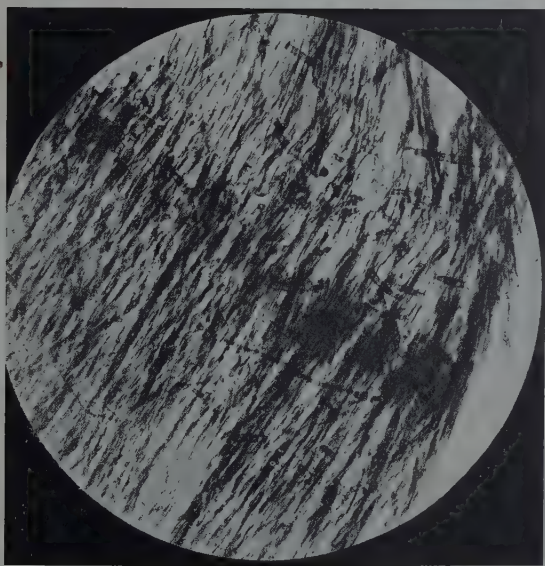


Fig. 10

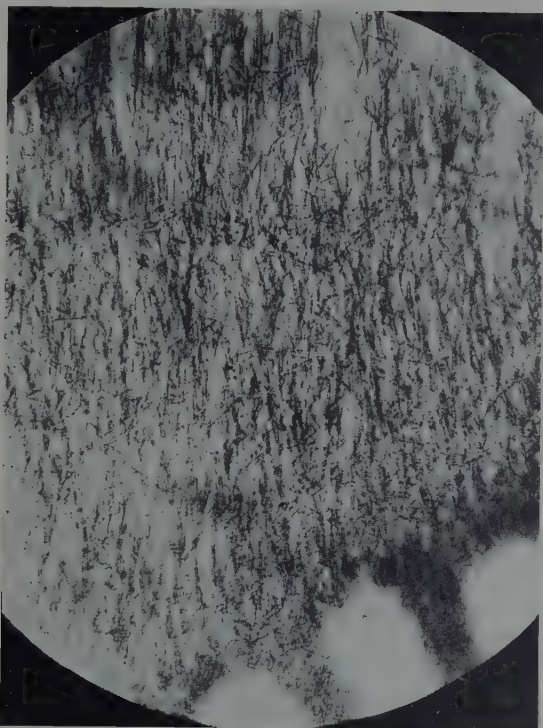


Fig. 11



Fig. 12

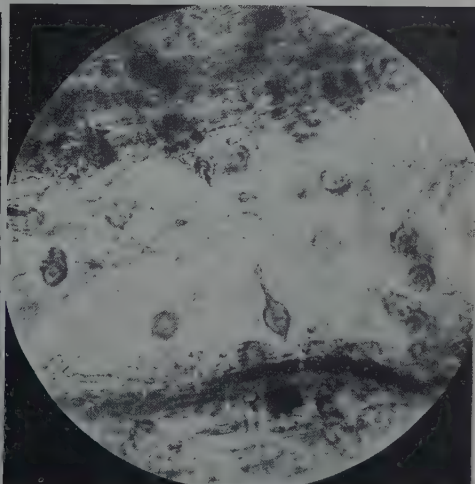


Fig. 13

NOTES

ENTOMOSPORIUM MACULATUM ON PEARS

By J. PERLBERGER

Division of Plant Pathology, J. A. P. Agr. Res. Sta., Rehovot.

A leaf disease hitherto unknown in Palestine appeared in spring 1939 in four pear nurseries in the northern part of the country. All the trees affected had come from the Government nurseries at Acre and were on *Pyrus syriaca* stock.

Small round brown spots, slightly prominent, appear especially on the upper side of the leaves. These spots attain a size of not more than 1—2 mm. Many brown spots may appear on one leaf, where they may coalesce into bigger areas, and the leaf tissue between the spots also turns brown. Leaves which have been affected and turned brown are then shed. After a short time the trees are stripped of all their leaves, only a few green leaves persisting near the crown. In consequence of the shedding of their leaves the trunk of these trees fails to develop normally and they remain slender and small.

The cause of this disease has been identified as the fungus *Entomosporium maculatum* Atk. (Lev.). This fungus is known throughout the countries where pears and quinces are grown as causing the spotting and wilting of leaves. It has been reported from the United States, Central and Northern Europe, South Africa, and Australia. In Mediterranean countries it has so far been observed only in Spain, where UNAMUNO (Bol. Soc. Esp. Hist. nat. 35, 1935) first discovered it in 1935. The fungus represents the imperfect stage of the Ascomycete *Fabraea maculata* Atk. The mycelium of *Entomosporium maculatum* growing in layers below the leaf epidermis produces spores composed of four cells which are arranged in cross-shape. Two of the cells are larger, and two are smaller. The two small cells and the apical cell mostly possess long spines. The size of these spores somewhat differs from that so far determined in other countries. KLEBAHN (Haupt- u. Nebenfruchtformen der

Ascomyceten, 1918) states the spore size of the *Entomosporium* which he and others found on pear leaves, to be $14-20\mu$ in length and $7-9.5\mu$ in width, while the spores we found in Palestine measure $19-27.5\mu$ in length, and $4-11\mu$ in width. The large majority of spores is about 8μ wide. These measurements hardly warrant the assumption that we are dealing with a new variety of the fungus. In view of the fact that most of the investigations found in literature have been carried out on dry material while all our measurements were carried out on fresh leaf material, it would appear that our fungus is all the same identical with *Entomosporium maculatum*. (Fig. 1).

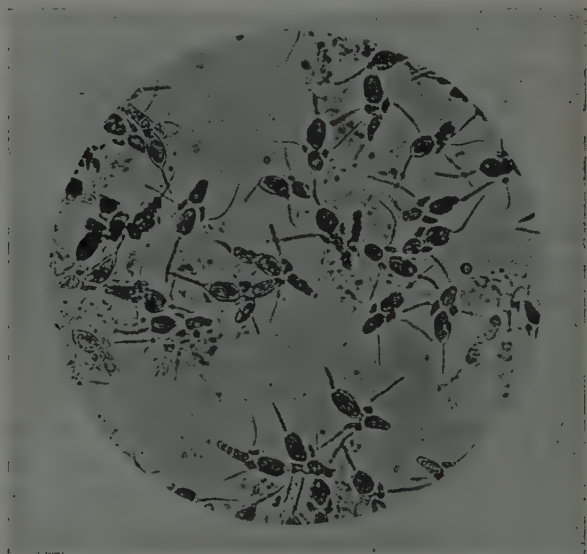


Fig. 1. Spores of *Entomosporium maculatum*.

It is surprising to find that the *Entomosporium* disease first appeared in Palestine on a pear native to this country (*Pyrus syriaca*), while it has so far, even last year, never attacked other varieties of pears (*Pyrus communis*) introduced from abroad as stocks or scions in recent years; nor has it as yet affected any of the locally grown quince varieties which in other countries

often suffer severely from this disease (WORMALD, Ann. Rep. East Malling Res. Sta. 1925). Under Palestinian conditions all other varieties of pear and quince appear to be more resistant than *P. syriaca*. The phenomenon of the resistance of certain varieties has first been mentioned as early as 1878 by SORAUER (cf. KLEBAHN). In 1907, KOECK (cf. KLEBAHN) divided the pear varieties grown in Austria into those resistant and those susceptible to *Entomosporium*. The resistance of varieties originating in Central Europe possibly finds its explanation in the fact that pears introduced into Palestine from European countries have passed from a cold and moist into a dry and warm climate. It might further be assumed that only a local variety has been attacked by a local strain of the fungus which is not virulent enough to affect more resistant plants introduced from abroad. But both these assumptions require supplementary study.

THE CHOCOLATE SPOT DISEASE OF BEANS

By M. CHORIN

Division of Plant Pathology, J. A. P. Agr. Res. Sta., Rehovot.

The Chocolate Spot Disease, caused by the fungus *Botrytis fabae* Sard, appeared on bean plants in Palestine at the end of 1938. It was previously recorded here at Geva in 1925/26 and at Beit Alfa in 1935/36 in the months of February and April, but was then not diagnosed accurately. This disease occurs almost everywhere in England and has further been reported from Australia, Spain, Japan, Cyprus and Egypt. At certain periods it may greatly lower the yield of beans.

Until 1923 neither details of the disease nor the causal organism were known. In 1923 PAINE & LACEY (Ann. Appl. Biol. 10: 194—203), published a paper with a detailed description of the disease and concluded that the chocolate spots were caused by bacteria. Not until 1929 SARDINA (Mem. R. Soc. Espanola Hist. Natur., 15: 291—5, 1929) discovered that not bacteria but the fungus *Botrytis fabae* Sard, caused the chocolate spots on bean plants. He described in detail the appearance of the spots and the fungus, with a Latin diagnosis of the latter.

In Palestine the reddish-brown spots with greyish centre appear on the whole surface of the leaves of beans and on their stalks. The spots occur on both sides of the leaf but are more conspicuous on its upper side. The spots are superficial or occasionally somewhat sunk into the leaf tissue. They may be small and like brown dots, or they may coalesce into one big spot covering almost the entire leaf. In the latter case the leaves are blackened and finally shed; the stalks, too, blacken rapidly and the whole plant wilts and dies (Fig. 1).

SARDINA who, as mentioned above, first determined the chocolate spot disease to be due to a fungus, considered a new species of *Botrytis* to be responsible for it and named it *B. fabae*. IKATA (Jap.



Fig. 1. Bean leaves affected by Chocolate Spot Disease.

Journ. Bot. 7: 6, 1934) who studied the disease in Japan held the same view. But WILSON (Ann. Appl. Biol. 24: 285—288, 1937) proved that many strains of *Botrytis cinerea* Pers. may cause the disease. The size of the spores was according to SARDINA 15.2—24.3 μ by 10.9—18.2 μ ; according to NATRAS (Cyprus Agric. Journ. 30: 57—58, 1935), who found the disease in Cyprus, 13—20 μ by 9—18 μ . In our case the spores measured 17.5—

28μ by $9-14\mu$. The spores of our strain were thus a little longer than those of the strains in Spain and Cyprus. The spore size of the English strain is not mentioned in WILSON's paper. Only a comparative study of the strains would make it possible to establish their identity definitely.

WILSON who carefully studied the environmental factors favouring the infection of plants by the causal organism, found a surface film of moisture on the plant to be essential for infection. The minimum of atmospheric humidity required for infection was stated by SARDINA to be 85%, and by WILSON to be still higher. The optimum temperature for infection, according to WILSON, is 20°C , while at 25°C spores of the fungus do not even germinate at 95% humidity of the air.

All this indicates that ecologically the fungus is oceanic in character and thrives only where temperatures are low and atmospheric humidities very high. The occurrence of the fungus is therefore typically restricted to countries with an oceanic climate, such as England, Australia and Cyprus, or to localities not far from the sea shore as in Palestine and Egypt, where the fungus only appears in the cold winter months:

CYTOSPORA CHRYSOSPERMA ON POPULUS NIGRA.

By M. CHORIN

Division of Plant Pathology, J. A. P. Agr. Res. Sta., Rehovot.

In April 1939 the disease was found on three poplar trees in a garden in Tel-Aviv not far from the sea shore. The leaves of these trees yellowed and were subsequently shed so that the trees remained without any leaves. Numerous slightly prominent cankers formed on the trunk of the poplars. The branches dried up from their tip downwards and the trees succumbed after a short time. From the lesions slender pink threads of up to 2 cm length developed so abundantly that the affected portions of the trunk appeared as if coloured reddish-pink.

On examination these prominent red threads were found to be composed of the spores of the fungus *Cytospora chrysosperma* (Pers.) Fr. which grows as a parasite in the wood of poplars, causing it to dry and eventually to die off.

After the mycelium has developed in the bark of the tree for a few months the fungus begins to produce fruiting bodies in the form of slightly prominent pycnidia, which split the bark of the diseased area. These pycnidia contain masses of minute hyaline spores which are one-celled and $2-4\mu$ in size; as the spores mature they are extruded from the pycnidia in the form of reddish-pink threads which are called "spore horns" or "tendrils" but remain attached to the pycnidia (Fig. 1).

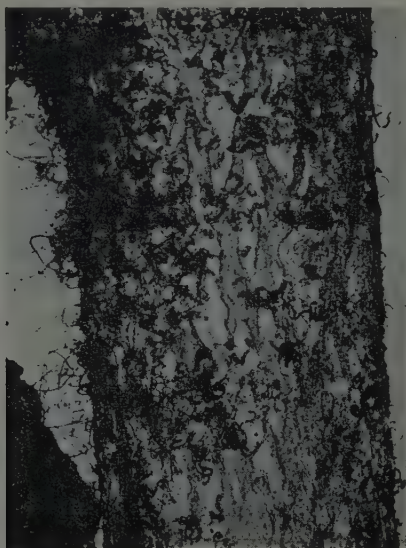


Fig. 1. Branches of *Populus nigra* attacked by *Cytospora chrysosperma*; "spore horns" protrude from the bark.

The fungus *Cytospora chrysosperma* appears mainly in the southwestern part of the United States, ranging from California to Canada. In Europe it has been reported to occur in Germany, Austria, Switzerland, Italy, France, and Sweden, and in Belgium (according to LONG, Journ. Agr. Res. 13: 331-343, 1918). It has

further been observed in South Africa, and now for the first time in Palestine. *C. chrysosperma* is, however, not known to occur in Russia.

The distribution of the fungus, as outlined above, proves it to be of widespread occurrence in countries with a moist oceanic climate. In Palestine the disease similarly occurred in the vicinity of the sea. It seems to have originated in the United States where it is very widespread and where it also possesses a wide parasitic amplitude, attacking trees of the genera *Salix* and *Acer* as well. In other countries it is found on species of *Populus* only.

MUENCH (Naturw. Zeitschr. f. Forst & Landw. 7, 1909) and SCHREINER (Journ. of Forestry 29, 1931) found the disease to occur under conditions unfavourable for the growth of the trees, e. g. under conditions of excessive drought; in Palestine it correspondingly developed where the soil was very dry and unfertilized.

SCHREINER discovered that *C. chrysosperma* constitutes part of the life-cycle of the fungus *Valsa sordida*. In Palestine, however, the perfect form has hitherto neither occurred in nature nor been produced in culture.

SHEMUEL YEDIDYAH

We regret to announce the sudden and premature death of S. YEDIDYAH, teacher in horticulture and founder of the botanical garden at Mikveh Israel.

Born at Suvalki (Poland) in 1895 in limited circumstances, YEDIDYAH came to this country in 1913 in order to study agriculture. During his studies he all the time had to earn his living as an agricultural labourer. After the Great War he went to California where he continued his studies at the Agricultural School of Davis. What he learned there made him, after his return, a pioneer of the introduction of Californian methods into the practice of citrus culture in Palestine. He was considered one of the outstanding experts in this field, and his excellent book on citrus culture ran to two editions. The latter so far represents the most detailed monograph available on the subject of citrus culture in Palestine.

In 1927 YEDIDYAH joined the staff of the old-established school of Mikveh Israel. His activities embraced the foundation of a rich collection of citrus varieties imported mainly from California, citrus root stock experiments, and studies of the problem whether or not the various strains composing the Jaffa orange variety remain true to type when propagated by vegetative methods. In these researches he followed in the steps of SHAMEL, who had carried out similar investigations of the Washington Navel and Valencia varieties in California. YEDIDYAH isolated and named a number of "off-types" of the Shamouti orange corresponding to similar types of the Washington Navel variety.

No less important were his contributions to the culture of subtropical fruit trees (such as the Avocado) and of deciduous fruit

trees which had previously met with little success in the coastal plain. He determined the identity of many varieties of fruit trees introduced some time before. We owe him the introduction of, among others, the olive varieties Ascolano, Sevelano, Manزالino and the plum varieties Beauty, Combination and Mariposa. YEDIDYAH paid special attention to the culture of local, European and Californian walnut varieties which he grafted successfully on *nigra* and *Hindsii* stock.

In 1930 YEDIDYAH planted the main part of the botanical garden of Mikveh Israel according to a plan outlined by Professor WARBURG. This garden which is essentially an arboretum containing numerous species of *Ficus*, *Quercus*, *Acacia*, *Eucalyptus*, *Conifers* etc. developed extraordinarily well under his supervision. In 1937 he built there a laboratory now called Beth Yedidiah where he arranged an herbarium of the species cultivated in the garden. Shortly afterwards he fell ill and died in spring, 1939. His death has left a gap which will be most difficult to close with a man of equal competence and activity.

H. R. O.

שמואל ידידיה ז"ל

מאת ה. ר. א.

הלך לעולמו המורה והמומחה הותיק לעצי הדר מר שמואל ידידיה. הוא נולד בסובלקי (פולין), בשנת 1895 ועלה לא"י בשנת 1913 כדי להכנס לחקלאות. הוא עבד שנים כפועל במושבות שונות ואחרי המלחמה נסע לקליפורניה כדי להשתלם בפרדסנות וגננות בביה"ס החקלאי העליון שבדיוויס.

ידידיה שב מצויד בידיעות רבות. נכנס כמורה לעצי הדר בביה"ס החקלאי שבמקוה ישראל, נטע שם פרדס יפה והתפרסם בידיעותיו הרבות. הוא כתב מאמרים רבים על זני עצי-ההדר שהוא הכניס מחו"ל ונטע במקוה ישראל, ועקב אחרי התפתחותם ותמורותיהם בארץ ישראל. מטע הזנים שלו במקוה היה יחיד בעשרו בארץ.

הוא הקדיש גם הרבה מזמנו לעצי פרי אחרים, נשירים וסובטרופיים, שהכניס למקוה ישראל מארצות שונות, ביחוד עצי זית ואגוז. הוא נטע גן בוטני לפי תכנית שהוכנה ע"י פרופ' רברורג ושישאר תפארת לארץ. עבודתו הגדולה הוא ספרו על גידול עצי הדר שיצא לו מוניטין בארץ.

יהי זכרו ברוך!

הדעה שבפטריה גנדרמה לוצידום, ואולי גם בפטריות שהם חקרו בעצמם, הקורים השלדיים נושאים את עצמם, ז. א. הם מתפתחים איזור אחד אחרי השני מהגידול ההילי הראשון והלאה. הם יוצאים ישירות מן הקצוות הפלסמטים של הקורים השלדיים של האיזור הקודם להם. הקורים של המערכת הזאת עוברים איפוא את שתי הדרגות הראשונות, דרגת הפלסמטית והבינונית, והם מקבלים לבסוף את הצורה השלדית או הסקלטית (ראה תמונות).

מחלת ה-*Entomosporium maculatum* על עצי אגס

מאת י. פרלברגר

המחלה הזו נמצאה השנה, 1939, בפעם הראשונה בא"י על שתילי אגס בר. הפטריה תוקפת את עלי האגס וגורמת ליצירת כתמים חומים כהים, שבעקבותם משחירים העלים ונופלים. רוב השתילים אינם מתפתחים בגלל הנשירה. הפטריה מזדהה כנראה עם זו שתוארה בחו"ל, היא נבדלת ממנה רק בזה שנבגיה יותר ארוכים וצרים (ראה תמונה). ארכם מגיע ל-19—27.5 מיקרונים באורך ו-4—11 מיקרונים ברוחב.

מחלת כתמי-שוקלדה על שעועית

מאת מ. חורין

בסוף שנת 1938 הופיעה המחלה הזו בא"י על עלי הפול. היא גורמת ליצירת כתמים אדומים חומים עם מרכז אפור ולנשירת העלים (ראה תמונה). גורם המחלה הוא הפטריה *Botrytis fabae* וילזון מצא שגם הפטריה *Botrytis cinerea* גורמת למחלה זו.

המחלה נתגלתה ראשונה בספרד ובאנגליה, אחרי-כן מצאה גם באוס-טרליה, יפאן, קפרוס, ומצרים. היא זקוקה בהתפתחותה לרטיבות יתרה שהיא מוצאת בארצות הנ"ל, כשהיא מתפתחת קרוב לים או במקומות הרחוקים מהים בימות החורף.

מחלת ה-*Cytospora Chrysosperma* על הצפצפה השחורה

מאת מ. חורין

המחלה הזו נתגלתה בשנה זו, 1939, על עצי צפצפה שגדלו בקרבת הים בתל-אביב. ענפי העצים מתיבשים מלמעלה למטה ולבסוף מת כל העץ. על הענפים נראים חורים ועירים שמהם מזדקרים חוטים אדומים המורכבים מנבגים של הפטריה הנ"ל (ראה תמונה).

המחלה מופיעה במערב ארצות הברית, באירופה התיכונית והצפונית. היא אוהבת רטיבות ומשום כך היא נמצאת בא"י רק בקרבת החוף.

דקת־הדפנות היוצרת את המחיצות; מערכת מקשרת המופיעה במקומות שונים של איזורי הגידול וסמוך לקליפה ולשפופרות; מערכת הפליסדות המכסה את הפרי; מערכת הפלקטנכימית היוצרת מין מקלעת בצורת ארגה המורכבת מתאים מרובי צלעות בהירים.

למערכות הקורים שמנינו ישנם התפקידים הפיזיולוגיים הבאים: המערכת השלדית מהווה את החלק הגופי של הפרי; המערכת היוצרת מחוללת את הקליפה ואת ההימינום או שכבת נבגי הבסיסה; המערכת המקשרה עוזרת להדוק את המקלע של גוף הפרי; מערכת הפליסדות משמשת כשכבת הגנה לגוף הפרי; והמערכת הפלקטנכימית מחזיקה ביחד את סוגי הארגה השונים של גוף הפרי. הקורים השלדים והיוצרים מתפתחים כל אחד לחוד מבלי להיות תלויים אלה באלה. הם מתבדלים בצורתם עוד בהיותם במצב גידול היולי (פרימורדיום). תכף ליציאתם מתפטיר המצעת שהם גדלים עליו.

גוף הפרי מתפתח אגב גידול־סירוגין המתבטא באופן ביולוגי בהתהוות חגורות בצורת קשתות בהירות וכהות המתפתחות חליפות והמהוות איזורי גידול הניכרים ונבדלים היטב. קורי הפטריה המתפתחים בלילה תפוחים בקצוותיהם, והקורים המתפתחים ביום הם צרים ובהירים בצבעם. קצוות הקורים הכהים מסתעפים בקצותיהם ובאופן כזה מוסיפים לאורך, רוחב ועובי של האיזורים הבאים. משערים שפהות קצות הקורים ותפחתם מתהווה בלידה ע"י הפעולה המעכבת של עתרת תחמוצת דו־פחמן ומחסור בחמצן באויר הכרוך בה בעץ ומסביבו בלילה, וע"י רבוי תמיסות הסוכרים בגזע העץ.

שתי הצורות של גוף הפרי, החד־רגלית והפרסית, מתהוות ע"י התפתחות מודרגת של איזורי גידול חצי עגולים העומדים כאילו על ציר מאונך לגבי המצעת. אם שטח המצעת הוא אפקי מתפתחת הצורה הראשונה; ואם הוא מאונך מתפתחת הצורה השניה.

בדיקת הגידים הלבנים העוברים בגופי הפרי של הפטריה הראתה שהם מתהווים ע"י פעולת ממיסה של קורי התפטיר הבאים מן המצעת והחיים כטפיל על גוף הפרי.

נעשתה השוואה בין התפתחות הפטריה גנודרמה לוצידום ובין התפתחות הפטריות המעוררות את נגעי הבית (*Merulius domesticus*) והטורטוריה (*Fomes levigatus*) שתוארו ע"י המלומדים פלק וקורנר. בניגוד לדעות החוקרים האלה המאמינים שהקורים השלדיים יוצאים מהקורים היוצרים, הובעה

בנובמבר 1934 היתה הפליטה מעל רק 10%—20% של הנידוף בכלל; בזמן של הנידוף העז ביותר, בשעות שלפני הצהריים, נצטמצמה הפליטה מעל עד כדי 4.5%—8%.

נידוף העלים בימי חמסין עלה לא בהרבה על זה שבימים הרגילים באותה העונה, ואילו האייוד בשעות היום של ימים כאלה נקבע כגבוה מן הרגיל עד לכדי 60%. החזיון הזה לא שונה גם ביום של חמסין מיוחד (בחודש מאי), ששלטו בו חום וחרבון מופלגים ושהצטיין בתנאים אטמוספריים בלתי-רגילים.

התצפיות מראות אצל עלי תפוח-הזהב כשרון רגולטיבי ניכר. הדבר מסביר את העובדה, שמין זה אפשר גידולו גם בתנאים האטמוספריים של אקלים צחיח למחצה. הפעולה המכוונת של הפיוניות תפקיד ראשי לה במערכת הגורמים, השומרים מפני מידה יתרה של איבוד מים לעזה.

בירור אנאליטי של המעלות והמורדות בעקומים לנידוף היומי ממד, שעוצם האור, קרינת-השמש הישרה ורטיבות האויר משפיעים השפעה כבירה על תהליך הנידוף, ואילו מהירות הרוח אינה בעלת השפעה במידה כזאת. הפעולה הרגולטיבית של הפיוניות, הנקצבת בכוח האור ובתקפו של מאזן המים בעלים, היא על פי רוב מכרעת לגבי ההפרשים שבין עקומת הנידוף של העלה לעקומת האייוד בכלל, — הפרשיהם, המצויים בשעות של חום-היום. בבחינה זו מגיעים המחברים למסקנות דומות לאלה של Stalfelt, בעוד שחקירת השפעתם של גורמי החוץ מביאה אותם לידי תוצאות שקבלו Shantz ו-Briggs.

מחקר אנטומי של פרי הפטריה *גֵּהוּקָה* (גנודרמה לוצידום)

הגורמת לרקבון עצים

מאת ישראל ריכרט וזהרה אביזוהר

(טבלאות xiv—x)

ניתן תיאור אנטומי של פרי הפטריה גנודרמה לוצידום שנאספה בא"י מששה עצים אכסנאים.

גידול הפרי יכול להיות בצורה חד-רגלית ואז יש לו כיוון פוטורופי חיובי או בצורת פרסה, ואז יש לו כיוון דיאגיאורופי.

אפשר היה לחלק את הקורים המרכיכים את הפטריה לחמש מערכות: מערכת שלדית או סקלטלית חסרת המחיצות ועבת-הדפנות; מערכת

עיקרה של שיטת המחקר היה בכך, שהעלים הקטופים נשקלו במאזני הובר שקילות אחדות בזו אחר זו, בהשתייה מועטה בין שקילה לשקילה. המאמר דן בשיטה מן הבחינה הבקרתית וההיסטורית. פעם בכל חודש נערכו המדידות, מלפני הנץ החמה ועד לאחר שקיעתה. אל השקילות נלוו תצפיות מטיאורולוגיות (עוצם האור, העניון, הטמפרטורות של האויר והקרע, רטיבות האויר, מהירות הרוח ומידת האיידר [לפי פיטש]) ופיסיולוגיות (מפתח הפיוניות, הערך האוסמוטי לעסיס התאי של העלים והגרעון לריווי המים של העלים). ניתנים תאור ודיון מקיפים, העומדים על כל הפרטים של המדידות והתצפיות הללו עם מסקנותיהן.

הוצאת המים ע"י העלה הנבדק מוסיפה ועולה אחר זריחת החמה עליה רהוטה, ובסוף 3—4 שעות היא מגיעה על פי רוב לשיא ראשון. בשעות הצהריים מתנוודים הערכים, ואחריהן, כ-3—4 שעות לפני השקיעה, מתחילה ירידה מוחלטת של הנידוף, הבא בזמן השקיעה עד לנקודת האפס בקירוב. הנידוף בשעות הלילה מועט מאוד, ואפילו בליל החמסין ירד שעורו עד אפס. עקומי-היום נתונים בצירורים 5—8; הם משתייכים לעתות-השגה השונות.

הגבהים המקסימליים, שעתות-השנה השונות מגלות, כמובן, זיקה מרובה אל התנאים האקלימיים השליטים, המשתנים מעונה לעונה. בשיאים ממוצעים של הנידוף בחמה נמצאו על ידינו בדצמבר — 300 מ"ג/גר', שעה (לגרם האחד של משקל העלה המלא, עם מימיו, ולשעה האחת). במרס — 489 מ"ג/גר', שעה ביולי — 975 מ"ג/גר', שעה ובספטמבר — 867 מ"ג/גר', שעה. ערכים מופלגים העלו המדידות ב-18 ביולי 1935, שעה 13, וב-18 באוקטובר 1934, שעה 9: הראשונה 1705 והשניה 1792 מ"ג/גר', שעה. כיון שהמים מהווים $\frac{2}{3}$ בערך מכלל משקלם של עלי תה", הרי המספרים האחרונים משמעם פחיתה של 2500 מ"ג בערך לגר' אחד של מים במשך שעה אחת. בלשון אחרת: כל אוצר המים שבעלה מתחלף תוך 24 דקות, אם מידת נידוף זו מתמידה זמן ממושך.

הכמויות הכוללות של הנידוף היומי בחמה ובצל מובאות בטבלה VII ובציור 10. הנידוף בצל העלה ערכים, שאינם מגיעים אלא למחצית רמתו של הנידוף בחמה. העלים השרויים בחמה הראו בחורף (דצמבר—מרס) מידת נידוף, שהיה בה כדי להיות במשך היום כמות מים בעלת משקל פי 1.3—2.5 ממשקלם המלא של העלים. באביב (מרס—יוני) עולה הכמות ההיא פי 4.3—6.5 מן המשקל הזה, בקיץ (יוני—ספטמבר) פי 6.5—9.5 ובסתיו (ספטמבר—דצמבר) פי 4.2—6.7. ברוב המקרים היה הנידוף של עלים צעירים מרובה משל זקנים. הנידוף מן הצד התחתון של העלה נמצאה גבוהה במידה חשובה מזו שמן הצד העליון. ב-21

את השטח שעליו גדלים צמחים בתנאים איקולוגיים שונים. אייג חידש את המושגים „צמחי הקשר” ו-„צמחים מרובי החבלים”. לראשונים הוא קורא כשהם גדלים בתנאים פחות או יותר דומים בשני חבלים סמוכים, ולאחרונים הוא קורא כשהם גדלים בחבלים שונים רחוקים זה מזה אבל בתנאי קרקע דומים.

אייג עשה הרבה בשביל הגיאוגרפיה הפלוריסטית. הוא עזר לחלק את האיזור החם-יבש של העולם הישן לחבלים פיטוגיאוגרפיים מיוחדים, כך מתחלק האיזור הזה לחבל מדיטרני הכולל את השטחים שגדל בהם תחורש; לחבל אירנו-טורני הכולל את הערבות; לחבל סהרו-סינדי הכולל את המדבריות ולחבל סודנו-דקני הכולל את השטחים הסובטרופיים. עבודתו הגדולה של אייג היתה החקירה הפיטוגיאוגרפית של א"י. הוא הציב גבולות לחבלים השונים המצויים בארץ וציינם במפה מיוחדת. הוא חקר באופן מיוחד את המובלעות (אנקלבות), ביחוד זה של חוף הים.

לשם הכרת הפלורה בתנאי הגידול הטבעיים של החבלים הפיטוגיאוגרפיים בא"י, הוא נסע לארצות הסמוכות: סוריה ועיראק, במקום שהצמחים עדיין גדלים בתנאיהם הטבעיים בלי הפרעה ע"י בני-אדם.

אייג התעסק גם בדברי ימי הצמחים. על יסוד שרידים בודדים ומסמכים ספרותיים הוא נתן תמונה היסטורית מהתפשטות אלון התבור ודברי ימיו בארץ. בזמן האחרון התעניין אייג במבנה הסוציולוגי של הצומח בארץ. הוא בדק באופן יסודי את חברות הצמחים באיזור החוף וגם גמר עבודה גדולה על כך. החומר על מבנה החברות בחבלים האחרים של הארץ עדיין לא עובד.

אייג גם התעניין בפרובלימות המעשיות הנובעות מגיאוגרפיה של צמחים. הוא האמין שאפשר על יסוד הצומח של השטחים השונים לקבוע את הצמחים שאפשר לגדל עליהם. אייג לא זכה להגשים את כל מאווי המדעיים ועייבונג הגדול עדיין מחכה לעיבוד.

על נידוף המים של עלי עצי ת"ז בפרדס

מאת ת. ר. אופנהימר וק. מנדל

מחקר ביואקלימי

המהלך היומי והמהלך השנתי של נידוף-המים בעלי עצי-ת"ז נחקרו במטע אחד שבאזור ההדר בארץ (על יד רחובות). העצים, שהעלים ניטלו מהם, היו בני שש שנים, מורכבים על לימון מתוק, והוחזקו בתנאי השקאה אופטימליים.

אייג הצליח מאד כמורה אקדמי. הוא היה מסור מאד לתלמידיו והצטיין במיוחד בסדור טיולים מדעיים בארץ ובמזרח הקרוב. הוא בקר בעבר הירדן, סוריה, דרום אנטוליה ובסיני. ע"פ הזמנת ממשלת עיראק ארגן מסע מחקר לקור-דיסטן בכדי להניח יסוד ביולוגי לעבודות היעור של הממשלה באיזור זה. בהודמ"נות זו חקר את צמחי המזון של הארבה במדבר סוריה.

אייג היה חלוץ בנין הארץ והמדע גם יחד. היה איש צנוע שהקריב את שעות חופשתו, מנוחתו, כספו ובריאותו למען התקדמות העם והמדע. היה חי בצמצום ויחד עם זה ידע לעזר לידידים ולתלמידים. הוא השיג גדולות בפרק הזמן הקצר שניתן לו ע"י הגורל לחיות, הודות למרצן המתמיד ולכשרונותיו היוצאים מהכלל כחוקר טבע. ראויים לציון מיוחד כשרונו המורפולוגי הנדיר אצל יהודים שאיפשר לו לברר הרכבם הסיסתמטי של קבוצות צמחים מסובכות, והבנתו המרובה בקשרים הקיימים בין הצמח ובין תנאי-קיומו. כשרון זה אפשר לו להכיר בשדה בין רגע את הגורמים האחראים לתפוצת הצמחים בבתי-גדולם, בין אקלימיים ובין אדפיים. הוא הדגיש את ערכו הרב של המחקר האקולוגי בפתרון בעיות סיסתמטיות מסובכות. שתי מטרות גדולות העמיד אייג לעצמו: אחת סיסתמטית: הכנת פלורה קריטית של הארץ והשניה אקולוגית נסיונית: ברור הגורמים החיצוניים הקובעים את תפוצת חברות הצמחים הטיפוסיים שלה. חובת חבריו בעלי המקצע שנשארו בחיים לגמר את מה שאייג לא הספיק להשלים.

בשנה תרצ"ו חלה במחלת מות ששמה קץ לחייו בחדש אב תרצ"ח. בן מ"ג היה במותו. מותו היא אבדה קשה ביותר למחקר הבוטני הצעיר. יהי זכרו ברוך.

אלכסנדר אייג כפיטוגיאוגרף

מאת ישראל ריכרט

ניתנה הערכת עבודתו הפיטוגיאוגרפית של המנוח אייג. תואר מהלך התפתחותו וההשפעות שהלו בו והתוו את דרך מחקרו. לרבותיו י. נ. וויולוף ברוסיה וי. ברוך-בלנקה במונפליה היתה השפעה מיוחדת עליו.

אייג עזר לברר את המושגים היסודיים שבגיאוגרפיה של צמחים: חבל(רגיון) ו"יסוד" (אלמנט) שהיו משובשים בפי החוקרים השונים. את שניהם הוא קשר בתנאי הסביבה או האיקולוגיה של הצומח בניגוד לקודמיו שקשרום לתנאים ההיסטוריים של הצומח ועוד. לפי אייג קוראים, איפוא, לצמחים המשקפים בגידולם תנאים איקולוגיים משותפים "יסוד" או אלמנט. ול"חבל" (רגיון) קוראים

עתון לבוטניקה

אלול תרצ"ט

סדרת רחבות

כרך ב' חוב' ב'

אלכסנדר אייג ז"ל

מאת ה. ר. אופנהימר

הלך לעולמו אלכסנדר אייג שיכול להחשב כאחד מאבות המחקר הבוטני בארץ: אחרי אהרונסון ואוטו ורבורג ז"ל.

אייג נולד בשנת 1895 במינסק ברוסיה הלבנה כבן למורה. בשנת 1909 עלה ארצה בכדי ללמוד חקלאות במקוה-ישראל. אחרי כן המשיך את לימודיו בגמנסיה הרצליה בתל-אביב. מימי נעוריו התעניין בטבע, ובמיוחד בצמח א"י. ביחד עם חברו פקטורי יצר מעשב חשוב שעורר את תשומת לבו של פרופ' ורבורג אשר הזמין בשנת 1923 לשמש לו כעוזר מדעי בתחנת הנסיונות החקלאית שהיתה אז בתל-אביב.

מאז התחילה תקופה פוריה בחייו המדעיים של אייג שנגמרה רק במותו. הוא הקדיש את כל כחותיו לחקר הצומח של א"י שחקר מבחינה פלוריסטית סיסטמטית ופוטוגרפית, ולבסוף גם פיטוסוציולוגית. במשך 15 שנה חבר שלשה ספרים וכ-40 מאמרים המטפלים בפלורה של א"י. מחקריו הניחו יסוד מדעי מוצק וחדש לידעת הצומח של א"י שלא נחקר כמעט לפניו מבחינה פיטוגוגרפית.

בספרו המוגרפי על הסוג בן-החטה *Aegilops* הראה כשרונות יוצאים מהכלל בסיסטמטיקה, לעומת זה התפרסם כפיטוגאוגרף בספרו על יסודות הצומח של א"י, בו נתן ראשונה נתוח אנליטי של כל המינים הפנרוגמיים הצומחים פרא בארץ.

אייג פרסם ועזב במותו עבודות מחקר מקיפות על קבוצות סיסטמטיות מסובכות של המזרח כגון *Anthemis Astragalus*. מלבד ורבורג השפיעו על התפתחותו המדעית בעיקר ווילוב ובראון בלנקי.

ב-1929 עבר לאוניברסיטה העברית בירושלים. שם ארגן את המחלקה לבוטניקה, קודם כעוזרו של ורבורג, אחר כך כראש מחלקה. ב-1938 זמן קצר לפני מותו נתמנה לפרופיסור באוניברסיטה העברית.

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עתון לבוטניקה

מופיע בשתי סדרות

א. סדרת רחבות:

יוצאת לאור ע"י ה. ר. אופנהימר וי. ריכרט של התחנה לחקר החקלאות, רחבות, איי. בכל שנה מופיעות 2 חוברות וכל חוברת נושאת עליה את תאריך הופעתה. כל כרך שנה מכיל מ-200 עד 250 עמודים.

ב. סדרת ירושלים:

יוצאת לאור ע"י חבר העובדים של המחלקה לבוטניקה באוניברסיטה העברית ירושלים (המנהל: ד"ר א. איג). בכל שנה מופיעות 4 חוברות וכל חוברת נושאת עליה את תאריך הופעתה. כל כרך שנה מכיל מ-300 עד 400 עמודים.

את דמי החתימה יש לשלם למפרע ע"י שק או המחאת דואר לפי הכתובת: המנהל של העתון לבוטניקה, ת. ד. 620, ירושלים. מחיר החתימה הוא:

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0,900 לא"י לשנה, בעד סדרת ירושלים בלבד

בסכום זה נכללים גם דמי המשלוח.

(מחיר חוברת בודדת 0,300 לא"י ושל כפולה 0,600 לא"י)

במכתבים הנוגעים לעניני המערכת של סדרת רחבות יש לפנות ל-"עתון לבוטניקה", ת. ד. 15, רחבות - ולעניני המערכת של סדרת ירושלים ל-"עתון לבוטניקה", ת. ד. 620, ירושלים.

במכתבים עסקיים, בכלל זה הודעה על שנוי כתובת, מודעות וכו', יש לפנות למנהל העתון לבוטניקה ת. ד. 620, ירושלים.

מן התכן של כרך ג'

מידת המיפתח של פיוניות (בקרת שיטת הפיקסציה של הפיוניות ע"י כהל). מאת מינה נדל

שרשי הדר: מבנם, ערכם האוסמוטי ותקופתיותם. מאת ק. קוסמן

נסינות בבקיעת היעור באלונים בא"י ע"י ה. ר. אופנהימר

גודל השת"ל הצעיר במשתלה מיסוד הסלקציה בלימון המתוק. מאת ק. מנדל

Sclerotinia minor על חסה ושעועית. מאת ד. סרני

רקבון העצים הגרם ע"י *Ganoderma lucidum* ותפוצתו הגאוגרפית. מאת י. ריכרט

מחלות עצי המגנו בא"י. מאת מ. חורין

נסינות מלחמה במחלת הכתמת (Mottle leaf) של עצי הדר. מאת י. פרלברגר

מינים חדשים של *Diploschistes* מערבות שונות. מאת י. ריכרט

ע ת ו ז ל ב ו ט נ י ק ה

סדרת רחבות

(לפנים רשימות לבוטניקה ומדעי צמחים)

יוצא לאור על ידי

ה. ר. אופנהימר וי. ריכרט
התחנה לחקר החטלאות, רחבות

ת כ ן

מוקדש לזכרו של פרופ' אוטו ורבורג

עמוד

ח	לזכרו של אלכסנדר אייג. מאת ה. ר. אופנהימר
ס	אלכסנדר אייג כפיטוגיאוגרף. מאת י. ריכרט
י	על גידוף המים של עלי עצי ת"ז בפרדס. מאת ה. ר. אופנהימר וק. מנדל
	מחקר אנטומי של פרי הפטריה בהוקה (<i>Ganoderma lucidum</i>) הגורמת לרקבון
יא	עצים. מאת י. ריכרט וז. אביזוהר
	רשימות :
יג	<i>Entomosporium maculatum</i> על עצי אגס. מאת י. פרלברגר
טו	מחלת כתמי-שוקולדה על שעועית. מאת מ. חורין
טו	<i>Cytospora chrysospermia</i> על הצפפה השחורה. מאת מ. חורין
טו	שמואל ידידיה ז"ל. מאת ה. ר. אופנהימר